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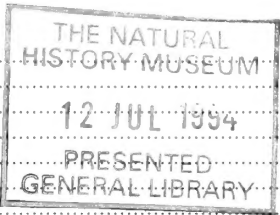
Systematics of the melicerititid cyclostome bryozoans; introduction and the genera *Elea*, *Semielea* and *Reptomultelea*

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CONTENTS

SYNOPSIS. The Family Eleidae, whose species are commonly referred to as melicerititids, is an unusual clade of cyclostome bryozoans with operculate zooids, a homoplasy shared with cheilostomes. Melicerititids range from the Barremian to the Palaeocene and are mostly European in geographical distribution. They are especially abundant and diverse in some Cenomanian-Campanian deposits of England, France and Germany. This paper is the first part of an intended comprehensive systematic revision of melicerititid species. Following a brief account of the history of melicerititid research and a review of their morphology, the main part of the paper describes 36 species belonging to the three fixed-walled genera (*Elea*, *Semielea* and *Reptomultelea*) with lamellar colony forms. Almost all of these species have been studied with the aid of scanning electron microscopy, and most of the type material has been re-examined and lectotypes chosen when necessary. The following 20 species are new: *Elea elegantula*, *E. flabellata*, *E. mackinneyi*, *E. pseudolamellosa*, *E. subhexagona*, *E. viskovae*, *E. whiteleyi*, *Reptomultelea acclivata*, *R. auris*, *R. bituberosa*, *R. convexa*, *R. goldfussi*, *R. levinseni*, *R. matutina*, *R. mitrus*, *R. parvula*, *R. pegma*, *R. pseudopalpebrosa*, *R. reedi* and *R. scanica*. *Reptomultelea betusora* is proposed as a new name for *R. tuberosa* (Reuss), a junior homonym of *R. tuberosa* d'Orbigny. Keys are provided for the identification of melicerititid genera, and for species of *Elea* and *Reptomultelea*.

INTRODUCTION

This is the first of a planned series of papers intended to provide a complete systematic account of the cyclostome bryozoan family Eleidae, commonly referred to as 'melicerititids' (Family Melicerititidae) and occasionally as 'operculate cyclostomes'. Melicerititids range from the Barremian Stage of the Lower Cretaceous to the Danian Stage of the Palaeocene, a duration of over 60 MA. Almost all species come from localities in Europe; melicerititids are presently unrecorded from the Americas, Africa, Antarctica and Australasia. They are important constituents of many bryozoan faunas, especially in the Upper Cretaceous of western Europe. However, melicerititids have never been comprehensively monographed, although Levinsen (1912) did revise many of the commoner species in the only major publication devoted to the group.

Melicerititids were chosen for detailed study for three principal reasons:

1. They clearly constitute a monophyletic group (clade), defined by the possession of a calcified zooidal operculum, and are therefore one of very few unequivocal clades which can be currently distinguished among cyclostome bryozoans or indeed stenolaemates in general. Questions concerning evolutionary patterns can be addressed with more clarity in monophyletic groups (see Smith, in press).

2. Melicerititids have a greater number of morphological characters for use in taxonomy than most other cyclostomes, principally because of the wide variety of apertural shapes and zooidal polymorphs they possess.

3. The operculum and avicularium-like polymorphs of melicerititids evolved in parallel with those of contemporaneous cheilostomes, providing an opportunity for comparative study of morphological and taxonomic diversification in two distantly-related groups of bryozoans.

These factors mean that melicerititids are a good target group among stenolaemate bryozoans for studies of evolu-

tionary patterns; for example, evolutionary trends, convergent evolution, and patterns of extinction and radiation.

HISTORY OF RESEARCH

The early history of research on melicerititids was fully chronicled by Levinsen (1912) and will only be summarized here. The first melicerititid species to be formally named was *Ceriopora gracilis* Goldfuss, 1826, from the Cenomanian of Essen in Germany. This species was subsequently assigned by Roemer (1840) to *Meliceritites*, the first genus to be proposed for a melicerititid. Roemer also assigned to his genus two other Cretaceous species, *Ceriopora roemeri* v. Hagenow, 1839 and a new species, *Meliceritites porosa*. The genus name *Meliceritites* was derived from the cheilostome genus *Melicerita* on account of their superficial similarity, notably in the hexagonal frontal shapes of the zooids.

The history of higher classification of the melicerititids began in 1851 when v. Hagenow referred *Meliceritites* (as *Escharites*) and *Inversaria* (now known to be a cheilostome, see Voigt & Williams, 1973; Voigt, 1974) to his division Salpingina, claiming to have identified opercula in both genera. Levinsen (1912) was probably correct in doubting v. Hagenow's claim: one of the species (*Escharites [Filicea] velata* v. Hagenow) in which opercula were supposedly seen by v. Hagenow lacks opercula but has terminal diaphragms that could have been mistaken for opercula. A year later d'Orbigny (1852) founded a division – Centrifuginés operculinés – for two of his new families, Eleidae and Myriozoumidae, making clear from the diagnosis that he had observed true opercula. While the Eleidae is nowadays the accepted family for *Meliceritites* and related genera of operculate cyclostomes, including the type genus *Elea*, the Myriozoumidae is recognized as a family of ascophoran cheilostomes.

Hamm (1881) included *Meliceritites*, together with two non-operculate cyclostomes (*Stigmatopora* Hamm and *Cyrto-*

pora Hamm), in the Stigmatoporina, a highly artificial division not adopted by later workers. Another disregarded group is the 'Typus' Metopoporina under which Marsson (1887) united the Eleidea [sic] and Ceidea [sic] based on their trumpet-shaped zooids (the remaining cyclostomes were placed in the 'Typus' Solenoporina). Despite the disuse of Metopoporina, the practice of grouping together these two families has persisted, notably in the *Treatise* (Bassler, 1953). Pergens (1890) referred the Eleidae to his Melicertitina.

Whereas Hamm (1881), Marsson (1888) and Pergens (1890) denied the presence of an operculum in melicerititids, Waters (1891) thought that only a chitinous operculum might have been present. Waters did, however, recognize the similarity between the eleozooids of melicerititids and cheilostome avicularia. Gregory (1899) confused opercula with terminal diaphragms (like several of his predecessors), but acknowledged the existence of 'avicularia', and observed brood chambers ('gonoecia' and 'gonocysts') in melicerititids. He also considered ceid cyclostomes to be merely worn specimens of melicerititids in which the frontal wall has been lost.

D'Orbigny's (1852) recognition of opercula was reaffirmed by Levinsen (1902). Lang (1906) very briefly revised the encrusting melicerititids, but his key to their generic identification is flawed in several respects. Thirty species and three varieties of melicerititids were described by Levinsen (1912) in a short monograph remarkable for the accuracy of its detailed observations and careful interpretations. Few advances have been made in understanding melicerititids since Levinsen's fundamental paper, although some papers have included systematic descriptions or figures of melicerititid species, notably those of Canu & Bassler (1922, 1926), Voigt (1924, 1928, 1951, 1953, 1960, 1962, 1967, 1973, 1975*a*, 1975*b*, 1981, 1983, 1985*a*, 1985*b*, 1989), Prantl (1938), Viskova (1965, 1970), Walter and coauthors (Walter 1975, 1977; Delamette & Walter, 1984; Masse & Walter, 1974; Walter & Clavel, 1979; Walter *et al.*, 1975), Brood (1972), Taylor (1987*a, b*), Pitt & Taylor (1990), and Favorskaja (1992).

Aspects of melicerititid morphology and palaeobiology were treated by: Boardman (in Boardman *et al.*, 1983), who reconstructed the soft tissues around the operculum; McKinney (1975), who described zooecial budding patterns of melicerititids and other dendroid stenolaemates; Taylor (1982), who described probable predatory borings in melicerititid zooids; and Taylor (1986*a*), who reviewed polymorphism in the group. More recently, Schäfer (1991) has described the gonozooids of melicerititids, and Taylor (1990) used melicerititids as an example of the application of scanning electron microscopy in bryozoology.

The systematic position of melicerititids within the Cyclostomata has received scant attention. Bassler (1953), in the bryozoan *Treatise*, grouped the Eleidae with the Ceidae (= Semiceidae Buge, 1952), placing the two families in the Suborder Salpingina. Viskova and Morozova (1988) and Viskova (1992) published an unorthodox classification which recognized three post-Palaeozoic orders of stenolaemates: Tubuliporida Blainville, Cerioporida Bronn, and Melicerititida Pergens. Within the Order Melicerititida they placed the families Eleidae d'Orbigny, Melicerititidae Pergens, Semiceidae Buge and Lobosoeciidae Canu & Bassler. There is little evidence to suggest a closer relationship between melicerititids and the two latter families than between melicerititids and several other tubuliporine families. Furthermore, partitioning the melicerititids between two families (Eleidae and Melicerititidae) rather than uniting them in a single family (Eleidae) implies an understanding of relationships between genera which is currently lacking; for example, it is unclear whether *Reptomultelea* (even if monophyletic) is more closely related to *Elea* than to *Meliceritites* (see p. 47).

General morphological comparison suggests that the sister group of melicerititids probably lies among non-operculate tubuliporine cyclostomes, notably *Collapora* and its relatives, which are traditionally assigned to the Family Multisparsidae (= Macroeciidae). Pending a comprehensive phylogenetic study, the Eleidae are here placed within the Suborder Tubuliporina Busk, 1852, although it is acknowledged that this suborder as currently understood is almost certainly paraphyletic.

MORPHOLOGY

The principal morphological characters observed in melicerititids are summarized in Table 1. Key features of melicerititid morphology are discussed below, with important terminology printed in **bold**, and the external appearance of zooidal polymorphs is depicted diagrammatically in Figure 1. It must be emphasized that the text below is not intended as a comprehensive account of all of the morphological variations found in melicerititids.

Colony-form

Despite the unusual morphology of the zooids in melicerititids, the range of colony-forms within the family is typical of

small eleozooid (demizooid)

intramural demizooid

autozooid with terminal diaphragm

autozooid with operculum

autozooid with open aperture

large eleozooid (rostrozooid)
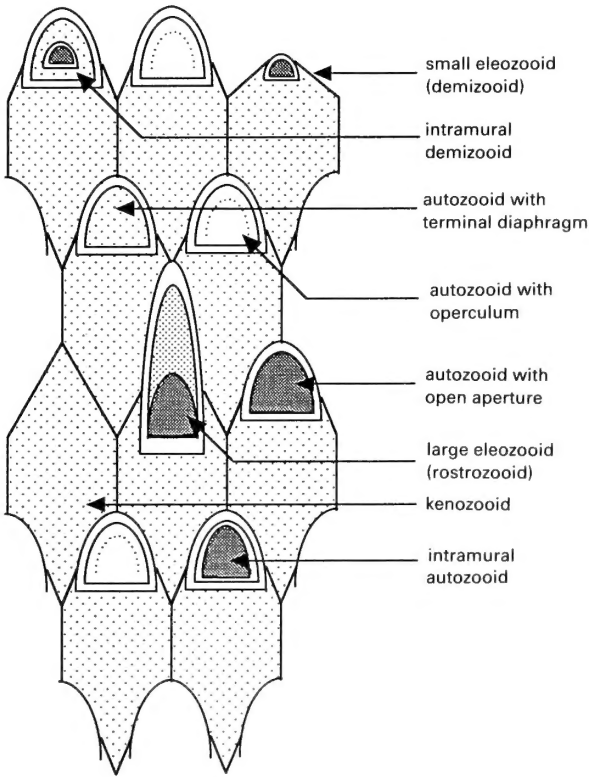
kenozooid

intramural autozooid

Fig. 1 Diagrammatic illustration of external zooidal morphology and polymorphism in melicerititid cyclostomes.

Table 1 Principal morphological characters of meliceritids.

Colony
a.   colony-form (encrusting, multilamellar, vinculariform without axial canal, vinculariiform with axial canal, adeoniform, eschariform, cavariiform)
b.   branch width/colony layer thickness
c.   overgrowths (presence, abundance, polymorph type of pseudoancestrula)
d.   base (extent, ancestrula, zone of astogenetic change)
e.   organization (fixed-walled, free-walled, mixed)
f.   zooid arrangement (whorls, quincunx, irregular, one side of branch only)

Autozooids
a.   frontal length
b.   frontal width
c.   frontal elongation (length:width ratio)
d.   frontal shape
e.   boundary wall
f.   aperture length
g.   aperture width
h.   aperture elongation (length:width ratio)
i.   aperture shape
j.   size of aperture relative to frontal area
k.   apertural shelf
l.   hinge teeth/bar
m.   abundance of in-situ opercula
n.   opercular pseudopore number and distribution
o.   surface ornament of opercula
p.   opercular sclerites
q.   terminal/subterminal diaphragms (abundance, placement, pseudopores, perforations)
r.   intramural buds

Eleozooids
a.–r.   of autozooids, and:
s.   affect on surrounding az (e.g. overgrowth, displacement)
t.   rostral platform

Kenozooids and cancelli
a.   distribution
b.   surface features

Gonozooids
a.   abundance
b.   total frontal length
c.   dilated frontal wall length
d.   frontal width
e.   frontal shape
f.   inflation
g.   ooeciopore length
h.   ooeciopore width
i.   ooeciopore shape (length:width ratio)
j.   atrial ring
k.   floor morphology

that encountered in many cyclostome groups. The following main colony-forms occur, in approximate order of frequency: erect dendroid (Figs 3, 5–7), encrusting multiserial and multilamellar (Figs 2,4, 181–184), erect bifoliate (Figs 17, 49,

87), erect tubular (Figs 110, 119, 121–123) and erect fenestrate (see Taylor 1987a). Common growth-forms of cyclostome bryozoans not represented among meliceritids are uniserial or pauciserial (ribbon-like) encrusting colonies, and articulated erect colonies.

All colonies begin with an encrusting base, usually attached to a hard substrate such as a shell (Figs 37, 134, 211) or pebble. However, some colonies were evidently attached to a perished organic substrate, leaving a mould bioimmuration usually in the shape of a hollow cylinder. In some cases, the edge of the original substratum was overlapped and the younger parts of the colony base grew freely over the sea-bed, becoming essentially free-lying (Fig. 183). Secondary substrates were occasionally incorporated into the bases of these free-lying colonies as they expanded across the sea-bed.

Erect growth is entirely lacking in species of *Reptomultelea* and the exclusively encrusting colonies are typically multilamellar (Fig. 4). However, the majority of meliceritid species developed erect growth from an encrusting base. Most erect colonies have subcylindrical branches, less than 2 mm in diameter, which bifurcate to give a dendroid, bushy colony (Figs 5–7) equivalent to the vinculariiform morphotype of cheilostomes. Species of *Meliceritites*, *Atagma*, *Meliceritella* and *Foricula* all have this colony-form. In most of these colonies, feeding zooids are evenly distributed around the circumference of the branches which, therefore, fall within the radial non-maculate category of McKinney (1986a, b). However, a few species with wider branches may develop raised **monticular maculae** (e.g. *Foricula aspera*). Multiple lamellar overgrowths are characteristic of many species with erect branches, particularly fixed-walled dendroid and broad bifoliate colonies. Branches of these colonies resemble the Jurassic cyclostome *Terebellaria* (Taylor, 1978) in cross-section, and may be termed 'terebellariiform'. In *Meliceritella* autozooids have a restricted distribution around the circumference of the subcylindrical branches which have a well-defined reverse or dorsal side composed of kenozooids and/or eleozooids. This colony morphotype therefore falls within the unilaminate category of McKinney (1986a, b). *Meliceritella* specimens are invariably recovered as short broken branches and it is usually uncertain whether colonies were originally bushy and three-dimensional or were almost two-dimensional planar fronds. However, scarcity of branch anastomoses suggests that most colonies were bushy with the exception of one species, *M. schneemilchae*, in which regular branch bifurcation and anastomosis in a single plane gives a fenestrate colony-form (Taylor, 1987a).

Less common among meliceritids are dendroid erect colonies with bilaminate branches in which zooids bud from both sides of a **median lamina** (Figs 26–27). Bilaminate colonies can have either narrow, strap-like branches which bifurcate in the plane of the budding lamina (e.g. *Elea elegantula*), or broad, foliaceous fronds which can be folded into complex corrugations or anastomosed into box-like structures (e.g. *E. lamellosa*). These occur in the fixed-walled

Figs 2–7 Colony forms in meliceritid cyclostomes. 2, multilamellar encrusting colony of *Reptomultelea sarthacensis* (d'Orbigny, 1853); EM RE 551.763.31.A711, Cenomanian, Essen, Germany; × 1·4. 3, typical assemblage of fragments of erect dendroid species; BMNH sample, Santonian, Craie de Villedieu, Villedieu, Loir-et-Cher, France; *ca* × 3. 4, worn edge of multilamellar colony of *Reptomultelea* sp. showing layering; EM RE 554. 763. 31. A745/9, Cenomanian, Essen, Germany; × 4·5. 5, erect dendroid colony of *Meliceritites dendroidea* (Keeping, 1883) embedded in a matrix of glauconitic sandstone; BMNH D3145, Aptian, Lower Greensand, Shanklin, Isle of Wight, England; × 0·8. 6, dendroid specimen of *M. dendroidea* with a densely-branched colony-form; BMNH D55269, Aptian, Faringdon Sponge Gravel, Little Coxwell Pit, Faringdon, Oxfordshire, England; × 2·2. 7, small, loosely-branched dendroid colony of *M. semiclausa* (Michelin, 1846) with a concave encrusting base of small area; BMNH D3695, Cenomanian, Le Mans, Sarthe, France; × 4·4.
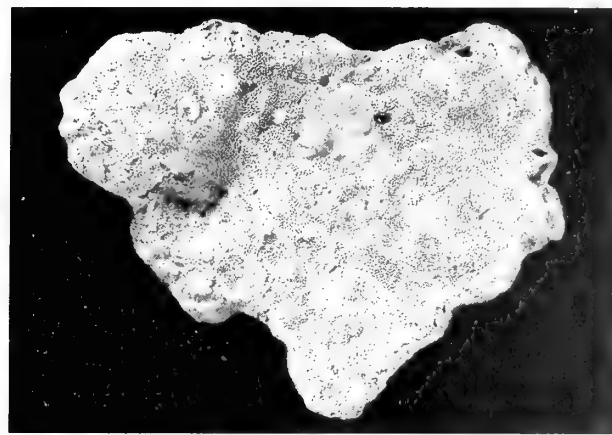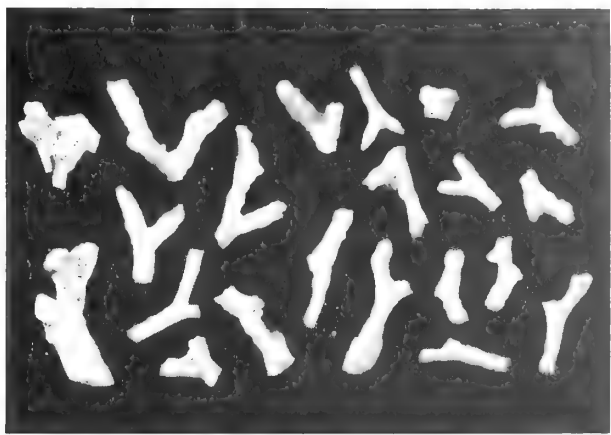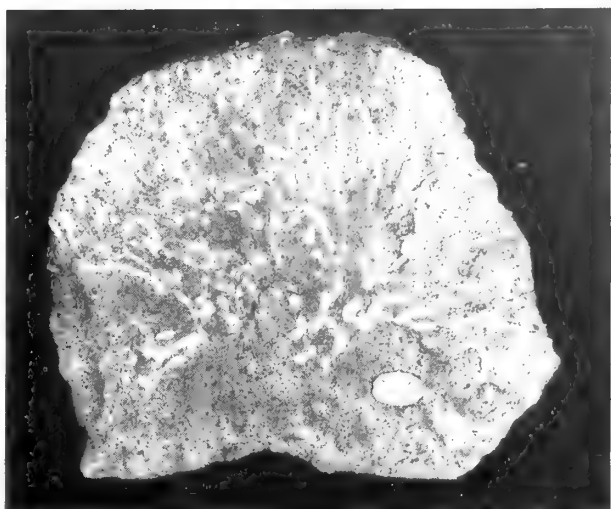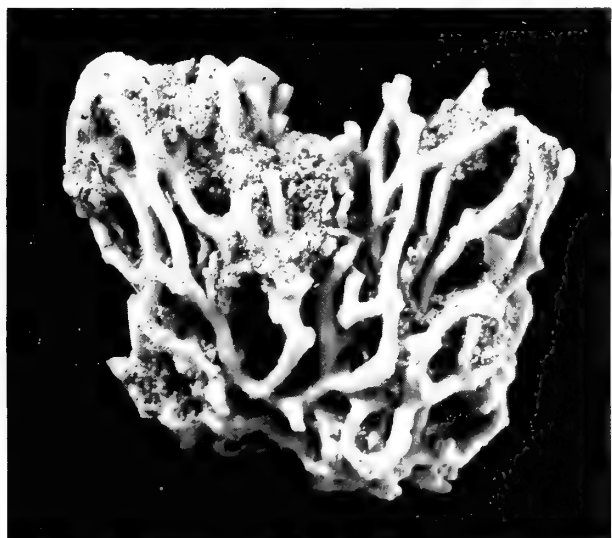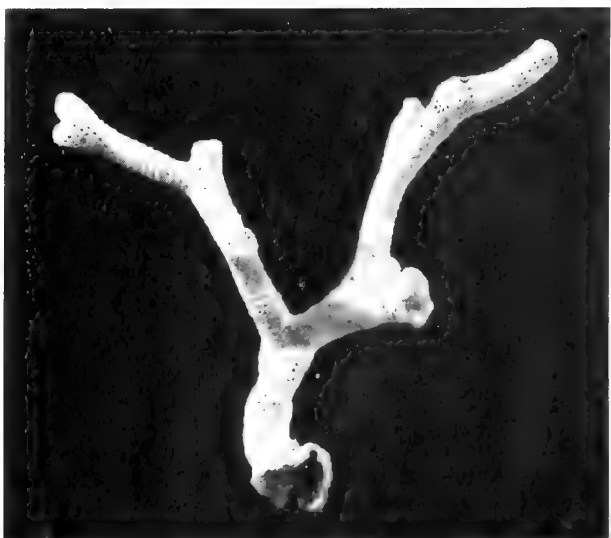
genus *Elea* and its free-walled analogue *Biforicula*.

Consistently tubular branches characterize the genus *Semielea*. The **axial lumen** (Fig. 119) of these branches is about 1 mm in diameter, and lined by an apparent exterior wall which is transversely wrinkled and whose origin can be traced back to the basal lamina of the colony base (Fig. 122). These 'cavariiform' branches seem not to be the result of growth around a perished substratum as the walls of the lumen evidently grew freely into space and do not bioimmure a substratum. Furthermore, the lumen is occasionally divided by transverse platforms which could not have formed in a colony wrapped around a cylindrical substratum (cf. *Lopholepis radians*, see Voigt, 1982: pl. 9, figs 3–6).

Much narrower **axial canals** occur in some species of *Meliceritites* (e.g. *M. semiclausa;* see McKinney, 1975: pl. 3, fig. 3a) but appear to be formed of interior rather than exterior wall. These resemble the axial canals found in the Mesozoic non-meliceritid tuliporine genera *Entalophora* (see Walter, 1970), *Bicoronipora* (see Walter, 1987), and *Coelospiropora* (see Voigt, 1968; Voigt & Flor, 1970; Walter, 1987), and in the late Palaeozoic cryptostome genus *Rhabdomeson* (see Blake *in* Boardman *et al.*, 1983). Axial canals of this type are of uncertain origin and function. Some may be greatly-elongated polymorphic zooids. It is possible that axial canals provided a pseudocoelomic connection of physiological value between branch growing tips and the older, more proximal zooids of the colony. Alternatively, their function may have related to the provision of a surface from which zooidal budding could occur.

Overgrowths can be found in most meliceritid species. They usually originate by intrazooecial fission (sensu Hillmer *et al.*, 1975) and subsequent eruptive budding of the newly-formed zooids onto the colony surface. Incipient overgrowths are first evident as apertures divided into an average of six chambers by radial walls arranged as spokes around an inner chamber enclosed by a ring-like wall (Figs 250, 271–272, 284). The inner chamber is apparently continuous with that of the parent zooid and develops into a **pseudoancestrula** at the centre of the overgrowth (Figs 131, 163, 179, 206–207, 212–213, 221, 225, 285). The pseudoancestrula is encircled by radially-orientated zooids originating from the surrounding chambers. A circular overgrowth with a circumferential growing edge is thus formed. Often several closely-spaced overgrowths are present and these coalesce as they grow outwards and come into contact with one another. Overgrowths are structurally distinct units and can be classified as subcolonies. Conspicuous secondary zones of astogenetic change are developed, beginning with the pseudoancestrula, which has a small aperture and little or no frontal wall. Aperture and frontal wall dimensions increase progressively through the succeeding generations of zooids. In species with high and pointed apertures (e.g. *Meliceritites gracilis* (Goldfuss)), zooids in secondary zones of change also tend to have proportionally shorter and more rounded apertures than zooids from zones of astogenetic repetition.

Skeletal organization

The major structural walls of bryozoan colonies can be categorized as basal walls, vertical walls and frontal walls. In all cyclostome bryozoans basal walls are apparently exterior walls, secreted from one side only, and include a calcified layer between the secretory epithelium and cuticle. Vertical walls and frontal walls may be with or without calcified layers. Three basic skeletal organizations (see Taylor & Larwood, 1990: fig. 10.6 for a simplified representation, and Boardman *in* Boardman *et al.*, 1983 for more detailed explanations of the latter two organizations) can be recognized according to which of these walls have calcification:

1. **Corynotrypid**. Known only in the Palaeozoic Family Corynotrypidae, this organization is characterized by calcified frontal exterior walls but non-calcification (or absence) of vertical walls.

2. **Fixed-walled**. Previously termed single-walled (Borg, 1926), fixed-walled organization has calcification of both interior vertical walls and exterior frontal walls. Frontal walls are fixed to the ends of the vertical walls.

3. **Free-walled**. Previously termed double-walled (Borg, 1926), here only the interior vertical walls are calcified. The frontal exterior wall remains uncalcified and is free of the vertical walls, enclosing a hypostegal pseudocoel between itself and the ends of the vertical walls.

Skeletal organization has been employed in the subordinal division of cyclostomes: two suborders (Tubuliporina and Articulata) are essentially fixed-walled, and three suborders (Cerioporina, Cancellata and Rectangulata) essentially free-walled. However, it is becoming increasingly clear that the taxonomic distinction between fixed- and free-walled cyclostomes is more complex. For example, the gonozooids of otherwise free-walled cerioporines are fixed-walled (e.g. Schäfer, 1991); individual branches of *Cinctipora elegans* can show alternations of free- and fixed-walled autozooids (Boardman *et al.*, 1992); and Boardman (1975) has described fixed-walled organization in a species of the normally free-walled genus *Heteropora*.

Meliceritids provide another example of the mixing of skeletal organizations. In all species for which they have been described, gonozooids are fixed-walled, whereas autozooids (and eleozooids) can be either fixed- or free-walled. Two meliceritid genera (*Foricula* and *Biforicula*) have free-walled autozooids, but the remaining genera possess fixed-walled autozooids. The areas between autozooidal apertures in free-walled genera are occupied by cancelli (Fig. 8). In contrast, the calcified frontal walls of the autozooids themselves occupy these areas in fixed-walled species (Fig. 8). Regardless of whether the free- or fixed-walled organization is the more primitive (see the inconclusive discussion in Boardman *et al.*, 1992), the existence of both organizations in the demonstrably monophyletic meliceritids shows that at least one of the organizational types must be polyphyletic in cyclostomes as a whole.

Zooid structure

Meliceritids are notable among cyclostome bryozoans for their high levels of zooidal polymorphism (Taylor, 1986*a*). Polymorphism is defined as discontinuous variation in morphology between zooids within a colony, and is known or inferred to reflect differences in function between zooids (see Boardman & Cheetham, 1973). Although different polymorphs are recognized morphologically, their naming in both Recent and fossil bryozoans is usually based on presumed function rather than homology (see Silén, 1977). This can be a difficult task in fossil bryozoans. A fundamental division is made between feeding zooids, termed **autozooids**, and non-feeding zooids, termed **heterozooids**. Sometimes two autozooidal polymorphs are present, for example the A- and B-zooids of the cheilostome *Steginoporella* (Banta, 1973).
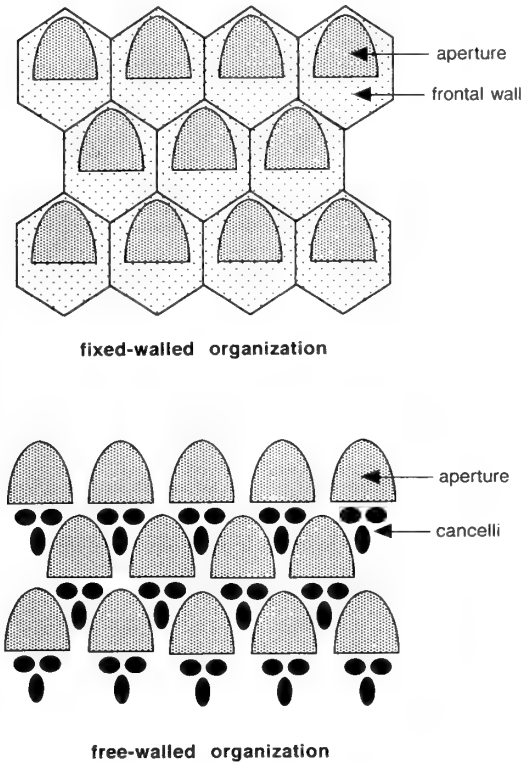
fixed-walled organization

free-walled organization

Fig. 8 Diagrammatic illustration comparing fixed-walled and free-walled organizations in meliceritidid cyclostomes.

Heterozooids in modern cyclostome bryozoans include **gonozooids** (sometimes called gynozooids to avoid terminological and functional confusion with androzooids; Silén, 1977), in which larvae are brooded, and **kenozooids** which is a 'wastebasket' category of atrophied zooids seemingly having space-filling roles. Both of these heterozooid types can be distinguished with relative ease in meliceritidids as they differ little from the same polymorphs in modern species of cyclostomes.

Most meliceritidids have an additional group of polymorphs characterized by opercula and apertures which are modified relative to other zooids in the colony. These have been termed **eleozooids** by Taylor (1986*a*), a derivative of Canu's (1897*a*) term 'eleocellaires'.

Internal morphology

Like most stenolaemates, the proximal parts of the zooids in **endozones** are long, narrow, thin-walled tubes orientated subparallel to growth direction (Fig. 9). With growth they gradually diverge from the branch axis and enter the **exozone**. At the endozone-exozone junction, zooids rapidly increase in width, their walls thicken, and they bend to become orientated almost perpendicular to the branch surface. Differences between meliceritidid polymorphs generally only become clear in the exozone and are much more apparent on the colony surface than in tangential or other sections cut through colonies.

Transverse sections of meliceritidid branches are notable for the strong contrast between the abundance of small diameter zooidal tubes in the endozone and the fewer large

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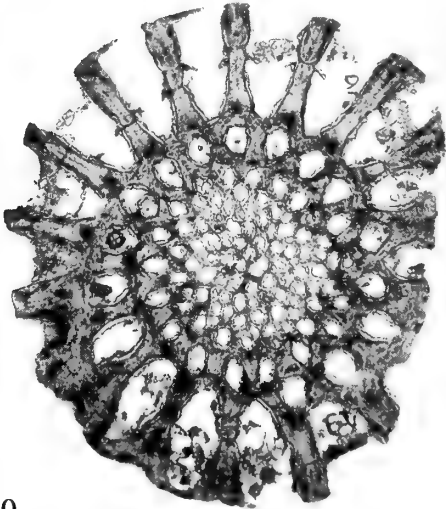
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Figs 9–10 Thin sections of a typical dendroid meliceritidid, *Meliceritites palpebrosa* Levinsen, 1912; USNM 2634–16, Coniacian [?Santonian], Villedieu, Loir-et-Cher, France; 9, longitudinal section showing long, club-shaped zooids originating in the endozone, × 16; 10, transverse section showing small diameter of zooids in the endozone and spiral arrangement of buds becoming evident at the endozone-exozone transition, × 40.

zooidal tubes in the exozone (Fig. 10). Budding of zooidal tubes occurs entirely in the endozone, with the exception of some very small polymorphs (e.g. demizooids in *Atagma*) and the cancelli of *Foricula* and *Biforicula*, which may bud in the shallower parts of the exozone close to the colony surface. Sometimes the zooids are arranged in spiralling rows in the outer endozone and exozone (McKinney, 1975; Fig. 10). At the bases of erect colonies and in unilamellar and multilamel-

lar colonies, new buds arise by division of vertical interior walls at their junction with a basal budding lamina of exterior wall. Bilamellar colonies have a similar style of budding but here the budding lamina is an interior wall (Figs 26–27). Dendroid colonies with axial canals may display budding around the periphery of the canal (McKinney, 1975: pl. 3, fig. 3a).

Intrazooidal structures are few within the endozone. Occasional thin **diaphragms** have been observed in some species (e.g. basal diaphragms in *Foricula* spp.), and **mural spines** are present deep within the endozone in zooids of *Elea triangularis* (Michelin) (Fig. 93). However, it should be noted that only a small minority of species have been studied in thin section and it is possible that internal structures are as yet undetected in other species.

Early astogeny

Early growth stages are known in very few species. While the bulk of melicerititid specimens are fragments from distal parts of colonies, those specimens which do preserve proximal parts generally have them completely obscured by the overgrowth of later zooids. Nevertheless, a few examples have been found of ancestrulae and succeeding zooids from the primary zone of astogenetic change. In all cases the **ancestrula** has a large protoecium (= primary disc) and a comparatively short distal tube (e.g. Fig. 288). This contrasts with most tubuliporine cyclostomes in which the distal tube is appreciably longer than the protoecium. Opercula have not been observed in-situ, but the straight proximal edge of the aperture strongly suggests that the ancestrula was operculate like the zooids of later astogenetic stages. The primary zone of astogenetic change shows the progressive increase in zooid size which is typical of early colony growth in bryozoans. Unfortunately, early astogeny is unknown in free-walled melicerititids and the presumed astogenetic transition between fixed- and free-walled organization has yet to be elucidated (cf. *Cinctipora elegans* as described by Boardman et al., 1992).

Autozooids

The outline shape of melicerititid autozooids varies between species but most often approximates a longitudinally elongated hexagon with two longer sides parallel to the long axis of the zooid (Fig. 11). Less commonly, autozooidal outline is 'rhomboidal', the proximal and distal sides at 90° to the long axis (Fig. 11). Four-sided, roughly diamond-shaped autozooids may also occur locally within colonies, apparently as derivatives of the hexagonal pattern in which the lateral sides have been eliminated. The distal angles of hexagonal zooids are variably rounded so that they are subparallel to the distolateral edge of the aperture, which is always positioned close to the distal end of the zooid.

Fixed-walled species have flat to slightly convex **frontal walls** pierced by pseudopores (by analogy with modern fixed-walled species, pseudopores would have been cuticle-covered during life). Whereas **pseudopore** shape varies considerably in other cyclostome groups, pseudopores in melicerititids are always circular; slit-shaped, teardrop-shaped and gull-shaped are unknown in melicerititids. The density of pseudopores characteristically declines approaching the apertural hingeline.

Zooidal boundaries vary in prominence in fixed-walled
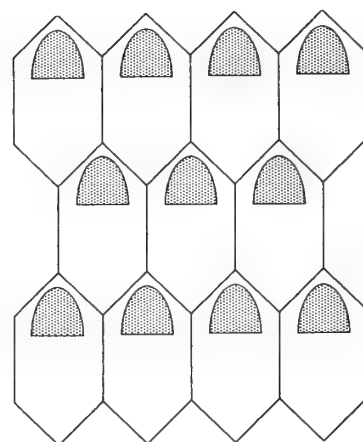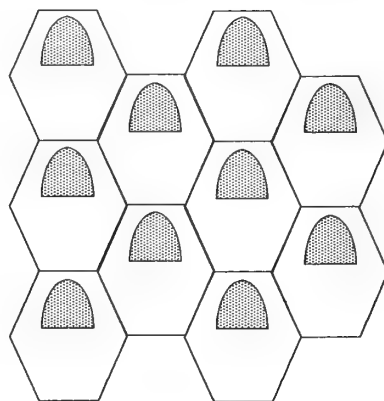
Fig. 11 Comparison between melicerititid cyclostomes with zooids of hexagonal and 'rhomboidal' surface outlines showing differences in the packing and arrangement of apertures.

species of melicerititids. Sometimes they are defined by a slightly salient wall lacking pseudopores, but in other instances pseudoporous frontal wall appears to extend uninterrupted across the boundary from one zooid to the next. Low, rounded **tubercles** may be formed from raised patches of zooidal boundary wall at the angles of the frontal walls in some species. Their location in hexagonal autozooids generally corresponds approximately to the two ends of the apertural hingeline and the distal tip of the aperture. In *Elea labyrinthica* (Michelin), a prominent tubercle is situated distally of the aperture (Fig. 61).

Autozooid **apertures** in fixed-walled species are positioned more-or-less terminally – no or very little frontal wall is present distally of the aperture. The shape of the aperture varies between species but is relatively constant within a species and provides an extremely useful character for species recognition (Figs 14, 125). Most species have apertures which are longer than wide, some have equidimensional apertures, and a few have apertures wider than long. The proximal edge of the aperture – the hingeline – is straight or slightly convex distally (bowed). The distal edge can be well-rounded, subrounded, sub-angular, or distinctly pointed. As a result,

apertural shapes found in meliceritids generally range from a semicircle at one extreme to a gothic arch at the other. More complex shapes are occasionally found, for example, the ogee-arch shaped apertures of *Reptomultelea sarissata* (Figs 282–283).

Hinge lines when well-preserved usually have a pair of small **teeth** or condyles, often with a ridge extending between them. Failure to observe these hinge teeth in some species is more likely to reflect preservational deficiency than true absence. *Meliceritites divergens* (d'Orbigny) is notable both for the large size of its hinge teeth and the presence of additional 'drop-like' teeth around the distal edge of the aperture (cf. the beading found on the distal edge of apertures in the cheilostome *Rhynchozoon*). **Apertural shelves** (e.g. Fig. 251) extend around the distal margins of the autozooidal apertures in many species of meliceritids and apparently form platform on which the closed operculum rested. Again, these vary in development between different species, ranging from barely discernable narrow shelves which are typically developed only in the distalmost parts of the aperture, to broad shelves of equal width along the entire distal margin of the aperture.

Compared with other cyclostomes, **peristomes** in meliceritids are extremely short and cannot readily be distinguished as a separate skeletal unit of the zooid. This contrasts with the long peristomes in *Plagioecia patina* and other tubuliporines which are marked by their sparse pseudopores and which may be shed as a unit during late ontogeny (see Silén & Harmelin, 1974). In the great majority of meliceritid species no more than a slightly raised apertural rim is developed. However, *Meliceritites dollfusi* Pergens has opercula located atop relatively well-defined but short peristomes.

Terminal diaphragms can be found in most meliceritid species but their distribution within colonies is generally without obvious pattern; seldom is there a clear ontogenetic zonation with terminal diaphragms in only the older, more proximal zooids, as found in many other cyclostomes (Silén & Harmelin, 1974; Boardman *et al.*, 1992). A variety of different types of terminal diaphragms can be distinguished, occasionally with more than one type being present in a single colony (or species). Some terminal diaphragms are pseudoporous (e.g. Fig. 178). These typically have a less-regular arrangement of pseudopores than is found in frontal walls. Non-pseudoporous terminal diaphragms may be planar or possess a central depression with pore (e.g. Fig. 238), reminiscent of the 'calcified terminal-vestibular membranes' known from other cyclostomes (Boardman & McKinney, 1976; Boardman *et al.*, 1992). In *Meliceritites lorieri* (Michelin) some zooids possess two or even three pores in the central depression. A third type of terminal diaphragm comprises an apparently simple, flat plate (e.g. Fig. 252). The exact location within the zooid of terminal diaphragms varies: some are positioned at about the same level as the operculum, but others are situated more proximally, occasionally beneath the apertural shelf (Fig. 252). Terminal diaphragms in relatively proximal positions may underlie in-situ opercula, as can be observed in thin sections or externally when in-situ opercula are damaged (Fig. 240). This implies that opercula do not necessarily have to be lost or shed before a terminal diaphragm can be secreted.

Calcified **opercula** (Fig. 12) are known or inferred to be a feature of all species of meliceritids. In most species they are commonly found in-situ, but in a few species in-situ opercula are extremely rare (e.g. *Meliceritites transversa* Canu &

Bassler). Opercula are occasionally found very close to the growing edge of the colony, sometimes within incompletely-formed apertures. Meliceritid opercula are undoubtedly exterior walls (i.e. with cuticle-covered external surfaces during life), even in the free-walled genera *Foricula* and *Biforicula*. However, their microstructure and ultrastructure differs from that of exterior frontal walls. The outer surface of exceptionally well-preserved opercula is marked by a series of radial fissures which are orientated parallel to local growth direction (e.g. Fig. 88). Poorly-preserved opercula often have a 'recrystallized' appearance with a strong fabric in the same orientation as these fissures (e.g. Fig. 101). Pseudopores are seemingly ubiquitous in meliceritid opercula but in only a few species are they near circular in shape and approximately evenly distributed over the surface of the operculum (e.g. Fig. 214). More often they are arranged in a crescent parallel to the distolateral edge of the structure and are slit-shaped, elongated parallel to local growth direction, (e.g. Figs 69, 88, 140, 186, 254). The inner surfaces of opercula possess a pair of ridges just inward of their lateral margins (Fig. 92). These ridges, termed **sclerites** by analogy with similar thickenings found in the opercula of cheilostomes, can be observed in sections of in-situ opercula, opercula dissected out of apertures, and are also sometimes visible as moulds left in the sediment filling the zooidal chamber after loss of the operculum (Figs 176, 266). Meliceritid sclerites are generally most pronounced close to the hinge line and become reduced distally. They often slope inwards towards the median line of the operculum. When the opercular pseudopores are arranged in a crescent, they are found to open immediately inwards of the sclerites. A shallow, dimple-like depression can often be seen on the outer surfaces of well-preserved opercula in the middle of the proximal edge, i.e. adjacent to the median bar of the hingeline in articulated opercula. External surfaces of opercula tend to lack ornament, although slight patterning is found in a few species (e.g. Fig. 58).

Autozooids with an additional rim within the main aperture are common in meliceritids (Figs 34, 45, 52–53, 55, 70, 89, 177) and were called regenerations by Levinsen (1912). This phenomenon should not however be confused with polypide regeneration, the routine process of formation of a new polypide (essentially gut and tentacles) by a zooid in which the old polypide has degenerated. Instead, analogy with cheilostomes (see Banta, 1969; Taylor, 1988) suggests that the 'regenerations' of meliceritids probably resulted from the budding of a new zooid within the skeletal chamber of a dead zooid and are better termed **intramural buds**. While autozooids are often budded intramurally into the chambers of old autozooids, eleozooids can also be intramurally budded into a host autozooidal chamber (Figs 19, 57, 111, 114, 156, 165, 171, 190, 195–196). Meliceritids are outstanding among cyclostomes in their high frequencies of intramural budding; Levinsen (1912) was able to point to only a few indistinct cases of 'regenerations' in *Entalophora madreporacea* and *Hornera lichenoides* among non-meliceritid cyclostomes.

Eleozooids

Meliceritid eleozooids are the morphological analogues of cheilostome avicularia in representing zooids with modified opercula (and apertures). However, whereas avicularia invariably have hypertrophied opercula, the opercula of
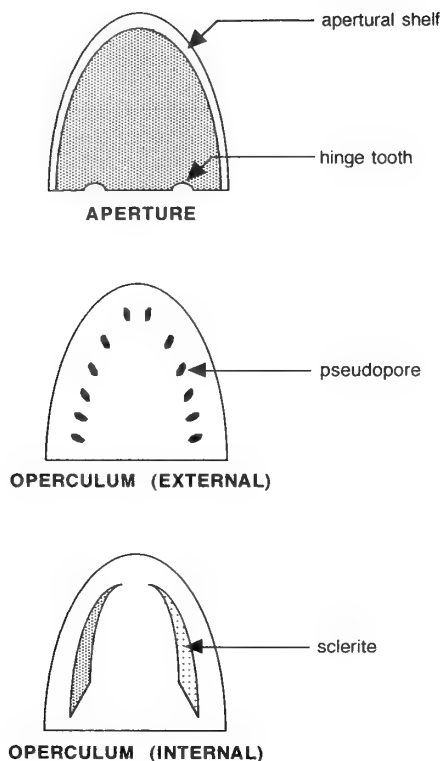
Fig. 12 Diagrammatic illustration of apertural and opercular morphology in meliceritid cyclostomes.

eleozooids may be hypertrophied or of reduced size relative to apertures of autozooids in the same colony. Eleozooids have no close analogues among modern cyclostomes but resemble the avicularia of cheilostomes. Avicularia are polymorphs with hypertrophied opercula, variously enlarged as mandibles or hair-like setae, and probably with a range of functions including defence, cleaning and even colony locomotion (see Winston, 1984, 1986, 1991). Normally, avicularia are heterozooids which are unable to feed, but occasionally they possess a feeding polypide and are therefore autozooidal polymorphs (Silén, 1977; Cook, 1979). Several different types of avicularia can be present within single colonies of some cheilostome species. Similarly, meliceritids may have several types of eleozooids within a single colony. There are frequently two types of eleozooids, one of which is larger and the other smaller than the autozooids in the colony. The restricted apertures of many eleozooids leads to the inference that they lacked a protrusible polypide, were incapable of feeding and are therefore classified as heterozooids. However, some of the larger eleozooids have apertures of sufficient size to have allowed protrusion of a polypide and it is possible that they were autozooidal polymorphs capable of feeding.

Three end-member categories of eleozooids can be recognized, termed rostrozooids, trifoliozooids and demizooids (Taylor, 1986a). Although most eleozooids are readily categorized into one of these types, some species possess eleozooids which are consistently difficult to classify. For example, the eleozooids of *Meliceritites magnifica* (d'Orbigny) (see Taylor, 1986a: fig. 2D) are rostrozooid-like in size but have trifoliate apertures, whereas the eleozooids of

Reptomultelea reussi (Pergens) (see p. 94) have the size of demizooids or trifoliozooids but apertures resembling rostrozooids. In addition, species with two types of eleozooids occasionally possess zooids with morphologies intermediate between the two types. In all three types of eleozooids, the frontal walls of fixed-walled species have an equivalent density of pseudopores as autozooids in the same colony. In this respect eleozooids differ from gonozooids which are characterized by a high density of pseudopores.

Rostrozooids (e.g. Figs 39, 48, 63, 142–145, 180, 201, 208, 223, 255, 295) have their apertures prolonged distally into a shelf-like platform, the **rostrum**. The frontal area of a rostrozooid typically exceeds that of an autozooid in the same colony, and the rostrum may occlude a distal zooid which would otherwise have apparently developed into a normal autozooid (i.e. the rostrozooid takes the position of two autozooids on the colony surface; see Boardman *et al.*, 1983: fig. 49.1 and 49.2). Zooids adjacent to the rostrum may be effected by its presence, sometimes developing as kenozooids (Fig. 143) and sometimes as autozooids but with obliquely-directed apertures (e.g., in *Meliceritites lorieri* the apertures of autozooids on either side of the rostrum are turned inwards towards the rostrozooid). Apertures of rostrozooids vary in morphology from almost semicircular and only slightly larger than an autozooidal aperture, to long and distally pointed, or long and distally rounded and with sides parallel or distinctly spatulate. In-situ opercula appear to be less common in rostrozooids than in autozooids, although this has not been tested quantitatively. Like autozooidal opercula, however, the opercula of rostrozooids often have a cresentic arrangement of slit-shaped pseudopores. Inner surfaces have been observed in only a few cases. Surprisingly, sclerites of the type seen in autozooidal opercula seem to be lacking in rostrozooidal opercula of *Meliceritites tuberosa* (d'Orbigny), although a marginal thickening does appear to be present. Rostrozooids are seldom arranged in regular or predictable patterns. In some species, however, rostrozooids may be clustered in groups of two or three, and they often occur in particularly high concentrations in the basal encrusting parts of erect species. Whereas frontal walls are lacking in the autozooids of the free-walled genera *Foricula* and *Biforicula*, it is notable that a small area of pseudoporous frontal wall is sometimes present in the rostrozooids. Together with the gonozooids, which are also fixed-walled in these genera, this gives colonies a mixed free-/fixed-walled organization within zones of astogenetic repetition. Intramural buds are commonly found within rostrozooids. These can be smaller rostrozooids (Figs 81, 145), trifoliozooids, demizooids or autozooids (Fig. 242). Multiple intramural rostrozooids commonly occur in some species, often with the distal ends of each successive rostrozooid being slightly elevated relative to the previous rostrozooid so that the aperture becomes inclined at a progressively greater angle to the colony surface. Two demizooids may sometimes occur as intramural buds within a single rostrozooid of *Atagma*.

Trifoliozooids (Figs 23, 164, 189) are distinguished by having apertures with a trifoliate opening in the shape of an inverted 'T'. On closer inspection of well-preserved examples, the opening is usually seen to be set within a D-shaped area which is occupied by the operculum on the few occasions that this is observed in-situ. Apertures are smaller than those of autozooids, sometimes only slightly so, however, ever. The frontal wall of trifoliozooids bears the same density of pseudopores as an autozooid and varies from a little

smaller to considerably smaller than that of an autozooid. Like rostrozooids, trifoliozooids may be concentrated in the encrusting bases of erect colonies. They may also occur with increased frequency in disrupted areas where crowding appears to have prevented the development of autozooids. Some species of *Meliceritella* have reverse (dorsal) branch surfaces composed of trifoliozooids, generally in combination with kenozooids. Trifoliozooids frequently occur as intramural buds within autozooids and sometimes within rostrozooids.

Demizooids are small eleozooids with simple D-shaped apertures and similarly shaped opercula. They show similarities to trifoliozooids in size, variation and distribution. Species of *Atagma* are particularly characterized by large numbers of demizooids which typically outnumber and may completely enclose the autozooids in the colony. Like trifoliozooids, demizooids can be found as intramural buds within both autozooids and rostrozooids.

Kenozooids

In fixed-walled meliceritids kenozooids are generally sealed by a calcified frontal wall, lack an aperture, and are identical in morphology to the kenozooids found in other tubuliporine cyclostomes. They are invariably smaller than autozooids and often more irregular in outline shape. Kenozooids are typically found in areas of growth disruption, including anastomoses (Figs. 228–229), bifurcations (Fig. 68), adjacent to gonozooids (Fig. 75) and eleozooids (Figs 143, 217), and also in the encrusting bases of erect colonies (Fig. 32). Some frontally-budded overgrowths commence with an apparent kenozooid and may include other kenozooids within the associated secondary zone of astogenetic change. Overgrowths of apparently open kenozooids, covering autozooidal frontal walls but leaving their apertures uncovered, are occasionally found in fixed-walled species (Fig. 79).

The small openings between autozooidal apertures of free-walled meliceritids were considered by Taylor (1986a) to be 'interzooidal spaces' rather than kenozooids because of their origin very close to the colony surface. These structures resemble the cancelli of hornerid cyclostomes and are accordingly given the same name. In neither meliceritids nor hornerids is the phylogeny of the group sufficiently well-known to determine whether the cancelli had an evolutionary origin as modified zooids or are non-zooidal in origin.

Gonozooids

Gonozooids, like those of many species of cyclostomes, are comparatively uncommon and have yet to be discovered in some meliceritid species. When known they are very similar to the gonozooids found in other tubuliporine cyclostomes, and also in articulate cyclostomes. Variation of gonozooid morphology within the meliceritids is slight. The distal frontal wall is bulbous, bears a high density of pseudopores, and in outline shape is usually longitudinally elliptical (e.g. Figs 24–25, 41, 65, 71, 78, 86, 262), occasionally more equidimensional (Fig. 236), and sometimes rounded-subtriangular with an almost straight distal edge (Fig. 209). Seldom do the neighbouring autozooids significantly indent the outline of the distal frontal wall (cf. Fig. 209), and they have never been found to pierce the frontal wall (cf. tubuliporines such as *Plagioecia*). Asymmetrical distal frontal walls are occasionally found in which the axis of the gonozooid

bends significantly from local colony growth direction and the ooeciopore opens laterally or obliquely.

The proximal end of the gonozooid appear identical to an autozooid – in fixed-walled species, it has a typically hexagonal frontal wall with the same density of pseudopores as an autozooid and a D-shaped opening similar to an autozooidal aperture. However, instead of being closed by an operculum, the D-shaped opening ('maternal aperture') forms the point of origin of the densely-pseudoporous distal frontal wall of the gonozooid (Fig. 42). Sometimes the distal frontal wall is initially a parallel-sided tube before dilation (Fig. 35), and in a few species (e.g. *Meliceritites dollfusi* Pergens) it grows proximally to cover the autozooid-like proximal frontal wall.

The ooeciopore is situated terminally and is usually transversely elliptical (Figs 138, 153, 166, 222, 292), less often subcircular (Fig. 65). Transverse width tends to be roughly the same as that of autozooids in the same colony. Rarely, the distal rim is prolonged into a slight tongue overhanging the ooeciopore. Significant ooeciostomes are lacking, even in well-preserved material where breakage can be ruled out. Teratological specimens include partially-formed, aborted gonozooids (Fig. 43), and coalesced gonozooids sharing a single ooeciopore (Fig. 147)

In all meliceritids with suitably broken gonozooids, a low ring diaphragm occurs in the distal part of the gonozooid just proximal to the ooeciopore (Figs 25, 71). This structure was first observed by Levinsen (1912) who termed it the **atrial ring** and noted the presence of a similar structure in the articulate cyclostome *Crisia eburnea* (Levinsen, 1912: pl. 7, fig. 12).

Removal of the roof allows the floor of the gonozooid to be examined. Traces of zooids which failed to reach the colony surface are visible through the basal wall of the gonozooid (e.g. Figs 24–25). The floor of the gonozooid may consist of a series of walls occluding the underlying zooids (e.g. Taylor, 1986a: fig. 3B). These overgrown zooids usually lack frontal walls, but in some cases possess a frontal wall and fully-formed D-shaped aperture (e.g. Levinsen, 1912: pl. 7, fig. 13), a condition found especially in zooids located more proximally beneath the dilated part of the gonozooid. Such features seem to indicate that development of the dilated part of the gonozooid was often retarded relative to the development of nearby autozooids.

Intramural buds have never been seen within gonozooids, nor have gonozooids been observed to originate as intramural buds.

STRATIGRAPHICAL DISTRIBUTION

The 36 species of fixed-walled lamellar meliceritids described here range from Albian to Campanian in age. Although species belonging to other meliceritid genera occur in the Barremian, Aptian, Maastrichtian and Palaeocene, there are no known species of *Elea*, *Semielea* or *Reptomultelea* in deposits of these ages. The peak diversity for lamellar meliceritid species occurs in the Cenomanian, which contains 17 species. Diversities of 7–9 species characterize the Turonian, Coniacian and Santonian, whereas the Albian and Campanian contain only 3 and 2 species respectively. This diversity pattern can be contrasted with the pattern for meliceritid species as a whole (Taylor 1986a, fig.

4; nb. constructed from a less complete database), which shows a Santonian peak in diversity. The anomalously large number of lamellar species in the Cenomanian probably correlates with the greater availability of nearshore localities, where species of *Reptomultelea* are particularly common.

Stratigraphical ranges of species of *Elea* and *Reptomultelea* are given in Figures 16 and 127 respectively. Most species are recorded from one stratigraphical stage only, but a few range through two or three stages. Better sampling will inevitably extend these ranges and caution should therefore be exercised when using meliceritids as age indicators.

SYSTEMATIC PALAEONTOLOGY

Specimen repositories and abbreviations. Specimens studied are housed in the following collections: BGS, British Geological Survey, Keyworth; BMNH, The Natural History Museum, London; DM, Dresden Museum (Reuss Collection); EM, Essener Museum; MNHN, Muséum National d'Histoire Naturelle, Paris; PSUB, Goldfuss Collection, Universität Bonn; SMD, Staatl. Museum Mineralogie und Geologie, Dresden; USNM, National Museum of Natural History, Smithsonian Institution, Washington; VH, Voigt Collection, Geologisch-Paläontologisches Institut und Museum, Universität Hamburg; ZMC, Zoologisk Museum, Copenhagen.

Methods of study. Almost all of the species described have been studied primarily using scanning electron microscopy (SEM), and whenever possible type specimens have been scanned. Application of SEM is becoming increasingly essential in bryozoology, both for the precise characterization of species and for their clear photographic illustration (Taylor, 1990). In the case of *Semielea dichotoma*, however, no material was available for SEM. Most SEM has been undertaken on uncoated specimens in an environmental chamber (Taylor, 1986b), using either ISI 60-A or ISI ABT-55 scanning electron microscopes. Unless otherwise stated, all of the scanning electron micrographs depicted here are images formed by back-scattered electrons (cf. secondary electron images which are more conventional in SEM of coated specimens, e.g. Fig. 180). It must be emphasized that the magnifications of these figures are very approximate because of highly imprecise machine readings.

Morphometrical determinations have been made using an eyepiece micrometer affixed to a Wild M7 binocular microscope. Time limitations have meant that for most species autozooidal dimensions have been determined from a single specimen only, preferably the holotype or lectotype. Intracolony variability within a species is therefore poorly known and deserves future study. Ten autozooids per colony have been measured in most species. Mean, standard deviation (SD), coefficient of variation (CV) and observed range are given. For eleozooids and gonozooids it has often been necessary to take measurements from several colonies to obtain a reasonable sample size. Figure 13 summarizes the principal measurements made on autozooids (and eleozooids); see Pitt & Taylor (1990: fig. 2) for comparable measurements made on gonozooids. When present in sufficient numbers, apertural measurements were made from zooids with in-situ opercula, as these have clearly-defined edges.

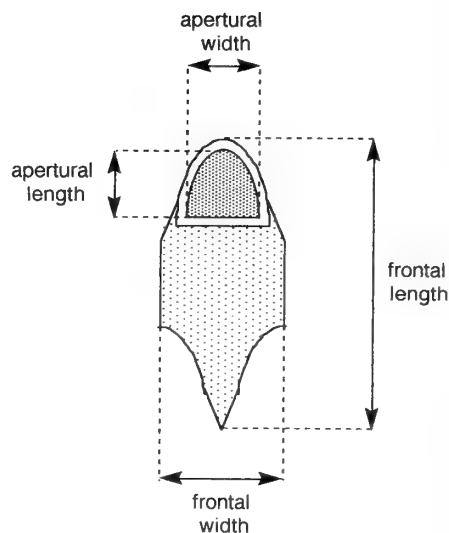Orientated thin sections (longitudinal, tangential and transverse) were prepared for a small number of species using a similar method to that described by Nye *et al.* (1972).

Fig. 13   Measured zooidal dimensions.

Order **CYCLOSTOMATA** Busk, 1852
Suborder **TUBULIPORINA** Milne Edwards, 1838
Family **ELEIDAE** d'Orbigny, 1852

REVISED DIAGNOSIS. Colony erect, dendroid, tubular, bifoliate or fenestrate; or encrusting, multiserial and generally multilamellar; overgrowths originating by intrazooecial fission and eruptive budding onto the colony surface, initiating a secondary zone of astogenetic change. Skeletal organization fixed-walled or free-walled, in some species varying according to polymorph type. Interior wall microstructure tripartite, apparently with a layer of transverse fibres flanked by lamellar layers. Ancestrula with a short distal tube. Zooidal polymorphism well-developed, most species possessing one or more types of eleozooids in addition to the autozooids, gonozooids and kenozooids. Autozooids fixed- or free-walled, operculate; operculum calcified, articulated with the straight proximal hingeline of the aperture, semicircular or arch-like in outline shape and bearing sclerites on the inner surface; peristome lacking. Eleozooids fixed- or free-walled, with opercula elongated to form pointed, rounded or spatulate mandibles in rostrozooids, reduced relative to autozooidal opercula in the smaller trifoliozooids and demizooids. Gonozooids non-operculate, fixed-walled with distal frontal walls densely pseudoporous and longitudinally elliptical (occasionally subtriangular) in outline shape, neither penetrated nor significantly indented by autozooids; ooeciopore terminal, transversely elliptical to subcircular; ooeciostome short; ring diaphragm (atrial ring) of low relief present just proximal to ooeciopore. Intramural budding common, often involving budding of a different polymorph type within the skeletal chamber of a host zooid.

REMARKS. The Family Eleidae d'Orbigny, 1852 antedates Meliceritidae Pergens, 1890 and, although priority is not mandatory with regard to family names, Eleidae is here

preferred but the term 'melicerititid' is retained for vernacular purposes.

Melicerititids have a clear autapomorphy in the possession of a calcified operculum, hinged to the proximal edge of the aperture and able to seal the zooid on closure. No other cyclostomes are known to have calcified (or uncalcified) opercula. The high level of polymorphism in melicerititids undoubtedly relates to the presence of this operculum which can be modified to form various polymorphs, analogous to the avicularia of cheilostomes derived by differentiation of the operculum (Taylor, 1986a).

Eight genera of melicerititids are recognized (Table 2). These are distinguished principally according to the traditional character of colony-form. A full phylogenetic analysis of the group will be necessary to determine whether zooid-level characters may be significant in an improved generic subdivision.

DISTRIBUTION. Barremian-Danian (or Montian), Europe and western Asia.

Genus *ELEA* d'Orbigny, 1853

TYPE SPECIES. *Bidiastopora lamellosa* d'Orbigny, 1850, designated by Gregory (1899, p. 299).

OTHER SPECIES. *Elea elegantula* sp. nov., *Elea flabellata* sp. nov., *Elea hexagona* d'Orbigny, 1853, *Eschara labyrinthica* Michelin, 1843, *Elea mackinneyi* sp. nov., *Elea pseudolamellosa* sp. nov., *Elea subhexagona* sp. nov., *Eschara triangularis* Michelin, 1841, *Elea viskovae* sp. nov., *Elea whiteleyi* sp. nov.

REVISED DIAGNOSIS. Eleid with bifoliate colony-form; autozooids with a fixed-walled organization; cancelli lacking.

REMARKS. D'Orbigny's (1853) original description of this genus emphasized its similarities to *Meliceritites* from which it was distinguished by the bifoliate form of the colony. Without choosing a type species, d'Orbigny included the following ten species in his new genus: *Diastopora cervicornis* Michelin, 1845, *Bidiastopora ramossisima* d'Orbigny, 1850, *Eschara ranvilliana* Michelin, 1845, *Elea calloviensis* sp. nov., *Elea reticulata* sp. nov., *Eschara triangularis* Michelin, 1841, *Elea rhomboidalis* sp. nov., *Elea turoniensis* sp. nov., *Elea lamel-*

Table 2 Key to melicerititid genera.

1.	Organization fixed-walled (i.e. autozooids with pseudoporous frontal walls; cancelli lacking) 2
	Organization free-walled (i.e. autozooids lacking pseudoporous frontal walls; cancelli present) 7
2.	Colony entirely encrusting .... *Reptomultelea*
	Colony erect 3
3.	Branches bilaminate, strap-like or frondose .... *Elea*
	Branches dendroid, circular or subcircular in cross-section .. 4
4.	Branches hollow .... *Semielea*
	Branches solid 5
5.	Autozooids absent on one side of branch .... *Meliceritella*
	Autozooids present around entire circumference of branch . 6
6.	Autozooids surrounded by numerous small eleozooids with D-shaped apertures .... *Atagma*
	Otherwise .... *Meliceritites*
7.	Branches bilaminate, strap-like or frondose .... *Biforicula*
	Branches dendroid, circular or subcircular in cross-section .... *Foricula*

losa sp. nov., and *Elea hexagona* sp. nov. The first four species are from the Jurassic and are not melicerititids; all four were placed in synonymy with *Multisparsa lamellosa* (Michelin, 1845) by Walter (1970). *Elea reticulata* from the Neocomian is also not a melicerititid. Walter (1985) assigned it to the tubuliporine genus *Mesenteripora*, as *Mesenteripora reticulata* (d'Orbigny, 1853). *E. turoniensis*, from the Turonian of Sainte-Maure (Indre-et-Loire), is represented by four specimens registered as No. 6964 in the d'Orbigny Collection, MNHN, including one specimen in a glass tube here designated as the lectotype (Voigt photocard 6959). This too is not a melicerititid. The remaining species listed by d'Orbigny are true melicerititids and are correctly assigned to the Family Eleidae.

Elea meridiana, described by Lang (in Woods, 1906: p. 283) from the Cretaceous [?Campanian] of Pondoland, South Africa is a bifoliate tubuliporine, not a melicerititid. Three figured syntype fragments are registered in the BMNH collections as D11834.

Among the eleven species validly assigned to *Elea*, a few subgroupings may be recognized. One subgrouping comprises *Elea elegantula* sp. nov. from the Lower Cenomanian, *E. subhexagona* sp. nov. from the Upper Cenomanian and Turonian, and *E. hexagona* d'Orbigny from the Santonian, three species with adeoniform colonies and very similar zooidal morphologies. They can be reasonably interpreted as members of a clade exhibiting an evolutionary trend towards an increase in the size of the autozooidal aperture relative to the frontal wall. *E. lamellosa* (d'Orbigny) and *E. pseudolamellosa* sp. nov. can be distinguished only by the morphology of the eleozooidal apertures which have an inverted T-shape in the former (trifoliozooid-type) but are D-shaped in the latter (demizooid-type). Other species of *Elea* (e.g. *E. triangularis* (Michelin) and *E. whiteleyi* sp. nov.) are very distinctive and more difficult to relate to congeneric species. *E. whiteleyi* from the Lower-Middle Cenomanian may be a member of the stem-group of *Biforicula*, judging by the similarity of its small eleozooids to those of the earliest species of *Biforicula*, *B. multicincta* from the Upper Cenomanian (see Voigt 1989). Table 3 is a key to the identification of species of *Elea* and should be used in conjunction with Figures 14 and 15, which show the characteristic outline shapes of the autozooidal and eleozooidal apertures respectively.

It is worthwhile speculating on the phylogenetic origin of *Elea*. Assuming that the genus originated from a fixed-walled ancestor, there are two main possible ancestral genera: *Meliceritites* and *Reptomultelea*. Origination from *Meliceritites* would require a change in the mode of erect growth from dendroid to bifoliate, whereas origination from *Reptomultelea* would require the acquisition of erect growth. The latter hypothesis is favoured for two reasons: (1) extensive *Reptomultelea*-like bases are often present in species of *Elea*, and (2) similarities exist between species of *Elea* and *Reptomultelea* in the shape of the acuminate eleozooids (rostrozooids). Full phylogenetic analysis is, however, needed. Stratigraphical distribution is not helpful in this respect as *Reptomultelea* and *Elea* both have their earliest known occurrences in the Lower Albian while *Meliceritites* ranges back to the Upper Barremian.

DISTRIBUTION. Lower Albian-Upper Campanian (Fig. 16) of France, Germany, England and Kazakhstan.
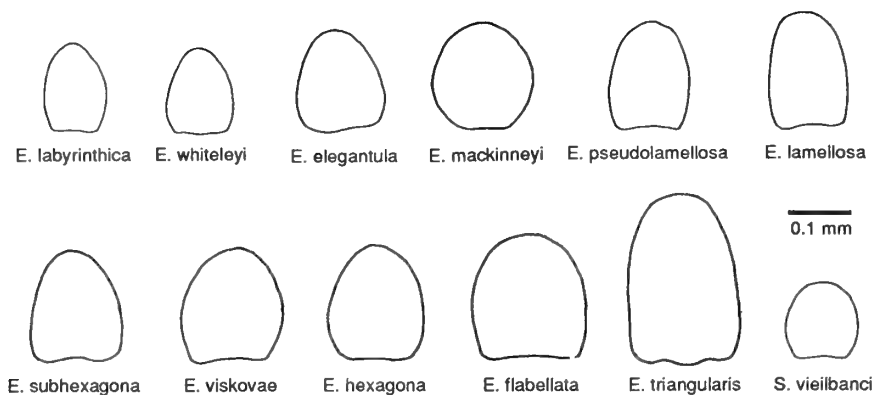
Fig. 14 Outlines of autozooidal aperture shapes in species of *Elea* and *Semielea*. Individual apertures were traced from SEM micrographs and scaled using the mean apertural length determined for the species. Species are arranged according to apertural length.

Elea lamellosa (d'Orbigny, 1850) Figs 17–28

1850 *Bidiastopora lamellosa* d'Orbigny: 266.
1851 *Bidiastopora lamellosa* d'Orbigny; d'Orbigny, pl. 625, figs 11–15.
1853 *Elea lamellosa* (d'Orbigny); d'Orbigny: 632.
1853 *Semielea plana* d'Orbigny: 638, pl. 738, figs 12–14.
?1853 *Reptelea pulchella* d'Orbigny: 642, pl. 738, figs 16–17.
1853 *Semimultelea irregularis* d'Orbigny: 652, pl. 741, figs 6–8.
1853 *Semimultelea gradata* d'Orbigny: 653 (partim), ?non pl. 741, figs 9–13.
1890 *Semielea plana* d'Orbigny; Pergens: 393.
1890 *Elea lamellosa* (d'Orbigny); Pergens: 398.
1899 *Reptelea pulchella* d'Orbigny; Gregory: 292, non fig. 31.
1899 *Elea lamellosa* (d'Orbigny); Gregory: 299.
non 1899 *Semimultelea irregularis* d'Orbigny; Gregory: 296, fig. 32.
1912 *Meliceritites plana* (d'Orbigny); Levinsen: 43, pl. 5, figs 11–12.
1912 *Meliceritites lamellosa* (d'Orbigny); Levinsen: 45, pl. 3, figs 1–9.
1985a *Elea lamellosa* (d'Orbigny); Taylor, fig. 2F and G.
1985b *Semielea plana* d'Orbigny; Voigt: 631, pl. 3, figs 16–17.

MATERIAL. Type: no type specimens have been designated; the d'Orbigny Collection, MNHN includes 8 glass tubes, all registered as 8191, each of which contains specimens of *Elea lamellosa* (e.g.Fig. 17). Some of these are from the two localities given in the original species description (i.e. Tours and Saintes); a lectotype could be selected from among these topotypic syntypes but the identity of the species is not in doubt.

Other material: MNHN d'Orbigny Colln 8191 (Voigt photocard 8310), Senonian [Santonian], Vendôme, France. MNHN d'Orbigny Colln 8195, specimen labelled by E. Voigt as the type of *Semielea plana* d'Orbigny (Voigt photocard 8319; figd by Voigt, 1985b: pl. 3, fig. 17), herein designated the lectotype of *S. plana*, Senonian, ?Tours, France. MNHN 8201 d'Orbigny Colln, specimen labelled by E. Voigt as the type of *Semimultelea irregularis* d'Orbigny (Voigt photocard 5733; figd by d'Orbigny, 1853: pl. 741, figs 6–8), herein designated the lectotype of *S. irregularis*, Senonian, Tours, France. BMNH D11786, Turonian, Touvent, Charente
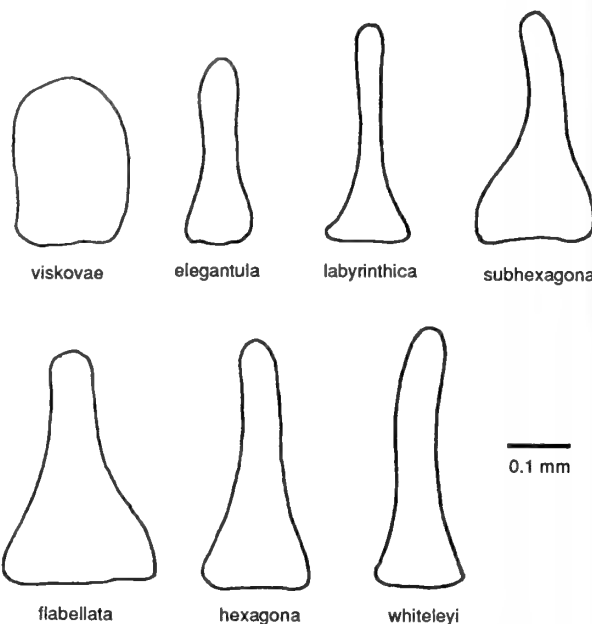

Fig. 15 Outlines of eleozooidal aperture shapes in species of *Elea*. Individual apertures were traced from SEM micrographs and scaled using the mean apertural length determined for the species. Species are arranged according to apertural length.

Inferieure, Jukes Browne Colln; D54296, Coniacian, Tours, Indre-et-Loire, Voigt Colln; D59166-7, Coniacian, Craie de Villedieu, Rue St Barthelemy, Tours, Taylor and Hammond Colln; D36195, Coniacian, St Paterne, Indre-et-Loire, Pergens Colln; D36176, Senonian, St Antoine-du-Rocher, Indre-et-Loire, Pergens Colln; D36060-2, Senonian, Vendôme, Loir-et-Cher, Pergens Colln; D53637, D59159, Coniacian or Santonian, Craie de Villedieu, Villedieu, Loir-et-Cher, Gale Colln; D59165, Coniacian or Santonian, Craie de Villedieu, Chateau Mbr, between Villedieu and Trehet on D80, Taylor and Hammond Colln; D58849 (sample), Santonian, Craie de Villedieu, Chateau Mbr, Bed 17 of Jarvis *et al.* (1982), Nowicki Colln; D58843 (sample), D59160-2, D59163 (sample), D59164, D59202-3, Santonian, Craie de Villedieu, Bouchardière Mbr, Bed 20 of Jarvis *et al.* (1982), Villedieu, Gale Colln; D58839 (sample), Santonian, Craie de Villedieu, Bouchardière Mbr, Bed 22a of Jarvis *et al.* (1982), Villedieu;

D59168 (sample), Santonian, Craie de Blois, Rue St Barthelemy, Tours, Taylor and Hammond Colln; D59169-72, Santonian, Craie de Saintes Fm., Voiville Mbr, les Arcivaux-Portublé, Saintes, France. USNM 2737–1 to 4, Coniacian, Villedieu (sections including duplicate acetate peels in BMNH). ZMC M40, [?Coniacian or Santonian], St Antoine du Rocher, France. ZMC Levinsen material unnumbered, Coniacian, Villedieu, Canu Colln.

Un-numbered VH material from the following localities: Coniacian, Tours; Coniacian, Villedieu; Coniacian, St Christophe, Indre-et-Loire; Santonian, Vendôme; Santonian, Merpins, Charente-Maritime; Coniacian, Joué-les-Tours, Indre-et-Loire (labelled *Semimultelea irregularis*).

DESCRIPTION. Colony normally bifoliate, foliaceous (Fig. 17), with broad, folded fronds (Fig. 18), about 0·6–0·8 mm deep, anastomosing and giving rise to daughter fronds perpendicular to their surfaces; overall shapes of complete colonies are flattened spheroids, up to at least 40 mm in diameter (e.g. BMNH D59159); parts of some colonies, including extensive colony bases, are unilamellar with a concentrically ridged exterior wall forming the basal side. Growing edges revealing several generations of buds, often occluded by a combination of small eleozooids and kenozooids. Overgrowths common, formed by eruptive budding onto

Table 3 Key to the species of *Elea*. Note that because this key places a high reliance on eleozooids, which may not be developed in every specimen, identifications should be carefully checked against the full descriptions; furthermore, it is possible that new material will reveal the presence of eleozooids in species in which they are currently unknown.

|	ALBIAN	CENOMANIAN	TURONIAN	CONIACIAN	SANTONIAN	CAMPANIAN
triangularis	—					
labyrinthica		—				
elegantula		—				
mackinneyi		—				
whiteleyi		——				
subhexagona				—		
viskovae				—		
lamellosa				?——	——	
flabellata					—	
hexagona					——	
pseudolamellosa						—

Fig. 16 Stratigraphical ranges of species of *Elea*.

1. Autozooidal aperture more than 0·25 mm long, bell-shaped; eleozooids unknown .... *Elea triangularis* (p.34)
   Autozooidal aperture less than 0·25 mm long 2
2. Eleozooids with long rostra (rostrozooids) present 3
   Rostrozooids lacking 10
3. Small eleozooids with D-shaped apertures (demizooids) abundant .... *Elea whiteleyi* (p.39)
   Demizooids lacking 4
4. A single large and prominent barkhan dune-shaped tubercle situated distally of the zooidal apertures ..... *Elea labyrinthica* (p.25)
   Otherwise 5
5. Reduced frontal wall occupying less than half of the autozooidal frontal surface; tuberculate zooidal boundaries .... *Elea flabellata* (p.20)
   Otherwise 6
6. Eleozooids with broad, well-rounded rostra 7
   Eleozooids with narrow, pointed rostra 8
7. Autozooids with broad apertural shelves; rostrozooid apertures less than 1·5 × longer than wide .... *Elea viskovae* (p.38)
   Autozooids with apertural shelf lacking or very narrow; rostrozooid apertures about twice as long as wide .... *Elea mackinneyi* (p.29)
8. Autozooids with a tubercle distal of the aperture .... *Elea hexagona* (p.23)
   Tubercle lacking 9
9. Autozooid frontal width less than 0·25 mm .... *Elea elegantula* (p.19)
   Autozooid frontal width more than 0·25 mm .... *Elea subhexagona* (p.32)
10. Eleozooids with inverted T-shaped apertures (trifoliozooids) .... *Elea lamellosa* (p.14)
   Eleozooids with D-shaped apertures (demizooids) .... *Elea pseudolamellosa* (p.30)
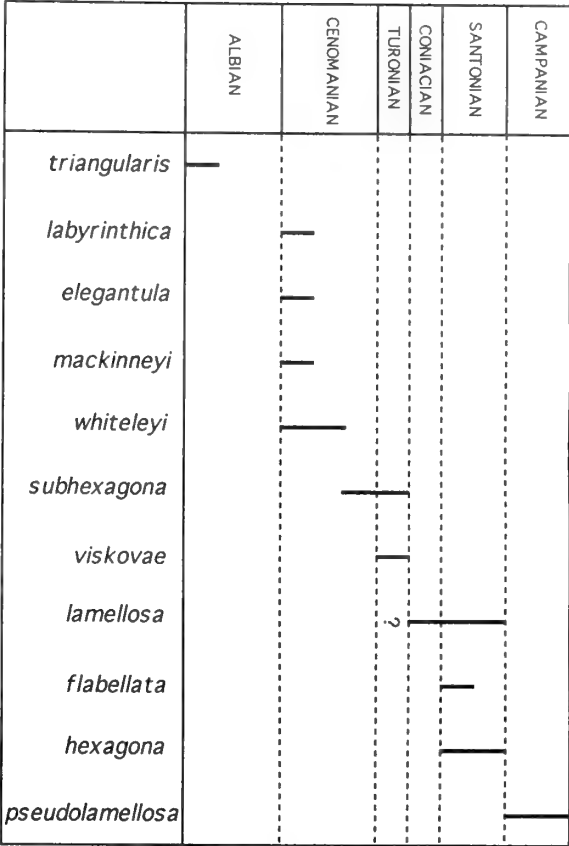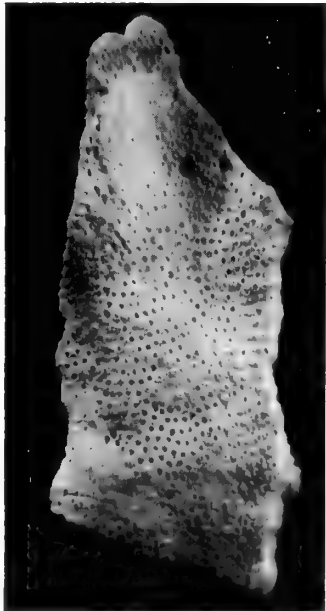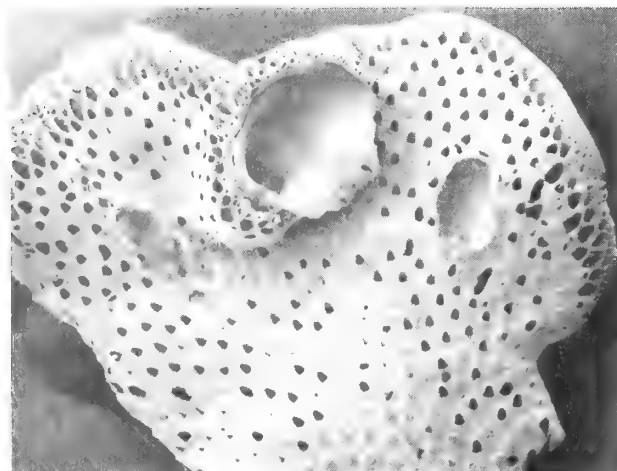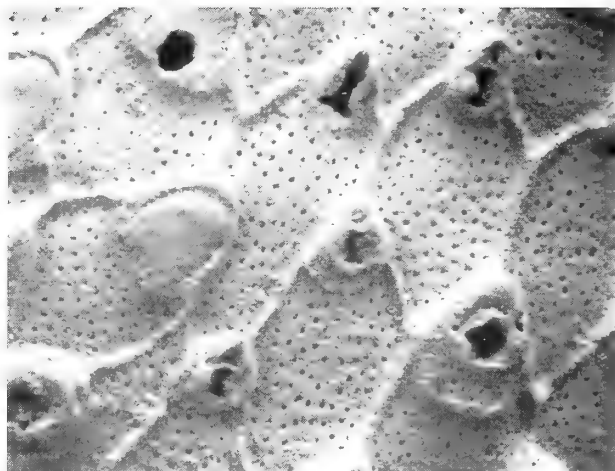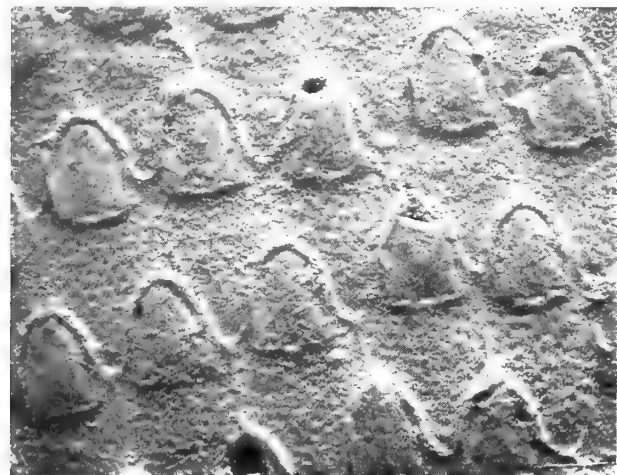
Fig. 17 *Elea lamellosa* (d'Orbigny, 1850), MNHN d'Orbigny Collection 8191 (Voigt photocard 8310), Senonian [Santonian], Vendôme, France; photograph of frond fragment, × 4·8.
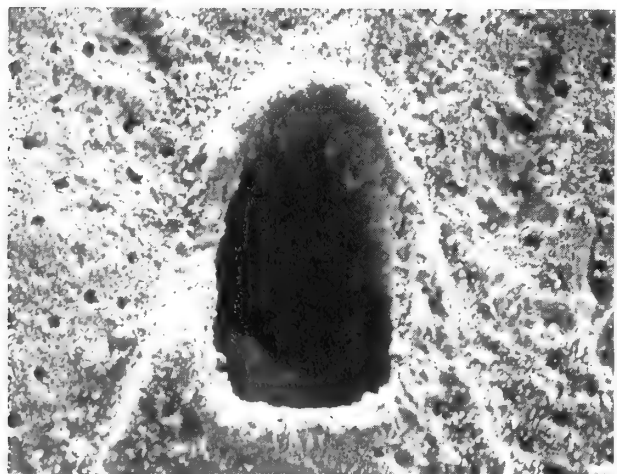
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the surface of a frond, initiating a zone of secondary astoge-netic change, becoming subcircular in outline; pseudoances-trula an autozooid; autozooids in zone of change in old overgrowths often with intramurally budded eleozooids. Zoo-ids generally arranged in quincunx; organization fixed-walled.

Autozooids (Fig. 20) medium-sized, frontally hexagonal or diamond-shaped, about 1·5 x longer than wide, outline extended distally and rounded by apertural rim; frontal wall flat or very slightly convex, with circular pseudopores; zoo-ecial boundaries distinct, raised. Apertures (Fig. 22) small, longitudinally elongate, 1·1–1·4 x longer than wide, attaining maximum width at or a little distally of the hinge line, well-rounded distally; apertural shelf narrow; apertural rim prominent, moderately broad, continuous with raised wall forming remainder of zooecial boundary; hinge line with median bar. Opercula (Fig. 21) very often preserved in-situ, prominent, surface convex, pseudopores not observed. Ter-minal diaphragms not observed. Intramural eleozooids (Fig. 19) common, their inverted T-shaped apertures slightly smaller than those of primary eleozooids and occupying the distal half of the host autozooid aperture, a slightly concave pseudoporous exterior wall fills the proximal part of the host autozooid aperture.

Eleozooids abundant, distributed widely across fronds, sometimes clustered in small groups (Fig. 19), frontally 1·5–2 × longer than wide, typically a little narrower and more pointed distally than autozooids but of about the same length; frontal wall with circular pseudopores in the same density as those of the autozooids. Aperture (Fig. 23) small, longitudi-nally elongate, about 1·5–2 × longer than wide, attaining maximum width at the hinge line, inverted T-shaped in outline through indentation of lateral margins by the rostral shelf. Opercula rarely preserved in-situ, longitudinally elon-gate, rounded distally. Intramurally budded eleozooids within host eleozooids not observed.

Kenozooids often present in association with eleozooids, generally with a smaller frontal area than other zooidal polymorphs.

Gonozooids (Figs 24–25) common, sometimes paired, large, longitudinally elongate; frontal wall with a short parallel-sided portion emerging from the maternal zooidal aperture, dilating into an ovoidal bulbous portion almost twice as long as wide. Ooeciopore (Fig. 24) transversely elongate, 2–2·5 × wider than long, in outline often kidney-shaped due to the presence of an indenting proximal hemiseptum. Atrial ring (Fig. 25) well-developed.

Thin sections show median budding lamina (Figs 26–27) straight to slightly sinuous, similar to the normal interzooidal walls in microstructure; zooecia up to at least 0·63 mm in total length; frontal walls thinning distally towards hinge line; opercula (Fig. 28) thin, often less than 0·015 mm in thickness, sclerites present; interzooidal walls about 0·015 mm thick near centre of branch, increasing to 0·03–0·05 mm near surface; basal diaphragms occasionally present in proximal parts of zooids.
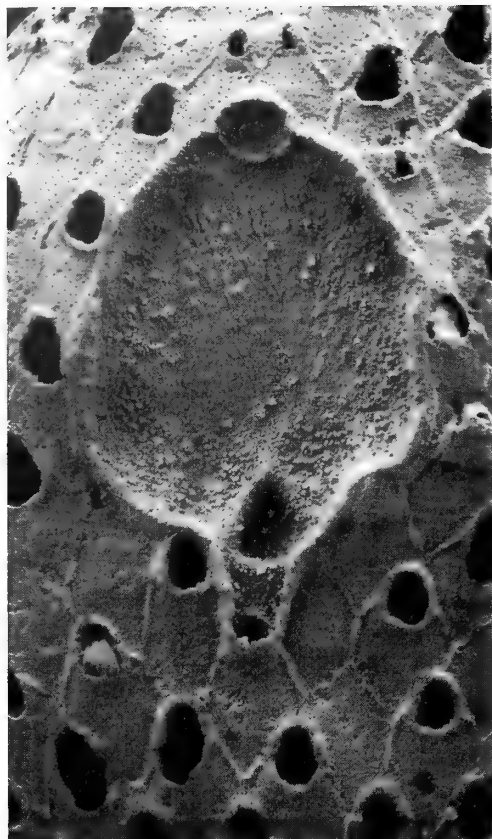

Fig. 24 *Elea lamellosa* (d'Orbigny, 1850), BMNH D59203, Santonian, Craie de Villedieu, Bouchardiére Member, Villedieu, France; de-roofed gonozooid with intact ooeciopore, × 45.

MEASUREMENTS.

autozooids (10 zooids with in-situ opercula from BMNH D59164)

frontal length:	mean = 0·49 mm; SD = 0·040 mm; CV = 8·2; range = 0·45–0·57 mm
frontal width:	mean = 0·32 mm; SD = 0·015 mm; CV = 4·9; range = 0·30–0·35 mm
apertural length:	mean = 0·19 mm; SD = 0·008 mm; CV = 4·2; range = 0·18–0·20 mm
apertural width:	mean = 0·16 mm; SD = 0·013 mm; CV = 8·1; range = 0·14–0·18 mm

eleozooids (10 zooids from BMNH D59164)

frontal length:	mean = 0·50 mm; SD = 0·054 mm; CV = 10·9; range = 0·42–0·59 mm
frontal width:	mean = 0·28 mm; SD = 0·046 mm; CV = 16·7; range = 0·18–0·33 mm
apertural length:	mean = 0·10 mm; SD = 0·008 mm; CV = 8·1; range = 0·09–0·11 mm

Figs 18–23 *Elea lamellosa* (d'Orbigny, 1850). 18, BMNH D53637, Coniacian or Santonian, Craie de Villedieu, Villedieu, Loir-et-Cher, France, frond fragment with two broken gonozooids and a partly enveloped, fouling oyster, × 7·5. 19, BMNH D59164, Santonian, Craie de Villedieu, Bouchardiére Mbr, Villedieu, primary eleozooids, operculate autozooids and a damaged intramural eleozooid (lower right), × 75. 20–21, ZMC Levinsen Collection M40, [?Coniacian or Santonian], St Antoine du Rocher, France; 20, regularly-arranged, operculate autozooids, × 74; 21, autozooidal operculum, × 220. 22–23, Santonian, Craie de Villedieu, Bouchardiére Member, Villedieu; 22, BMNH D59203, autozooidal aperture, × 285; 23, BMNH D59202, eleozooid aperture, × 330.

Fig. 25 *Elea lamellosa* (d'Orbigny, 1850), BMNH D59202,
Santonian, Craie de Villedieu, Bouchardiére Member Villedieu,
France; de-roofed gonozooid exposing entrance to maternal zooid
and atrial ring, × 45.

26

27

apertural width: mean = 0·06 mm; SD = 0·009 mm;
                          CV = 16·6; range = 0·05–0·08 mm

gonozooids (6 zooids from sample BMNH D59163)
total frontal length: range = 2·22–2·63 mm
distal frontal wall
length: range = 1·86–2·25 mm
frontal width: range = 1·10–1·31 mm
ooeciopore length: range = 0·08–0·11 mm
ooeciopore width: range = 0·17–0·20 mm

REMARKS. *Elea lamellosa* is an extremely abundant bryo-
zoan in the Coniacian-Santonian calcarenites of the Loire
region, notably the Craie de Villedieu, and in approximately
contemporaneous deposits in the Aquitaine Basin, for
example at Saintes. It is the only bifoliate melicerititid to
occur commonly in these beds, in which dendroid forms such
as *Meliceritites magnifica*, *M. ornata* and *M. tuberosa* tend to
dominate (Fig. 3). The foliaceous shape ('eschariform') of the
colonies contrasts with most other bifoliate melicerititids
which have strap-like branches ('adeoniform'). Although
present in several species of *Meliceritites* and also in *Semielea
vieilbanci*, no other species of *Elea* possess small eleozooids
with inverted T-shaped apertures. These trifoliozooids are
the principal means of distinguishing between *E. lamellosa*
and the closely similar but stratigraphically younger *E.
pseudolamellosa* (p. 30).
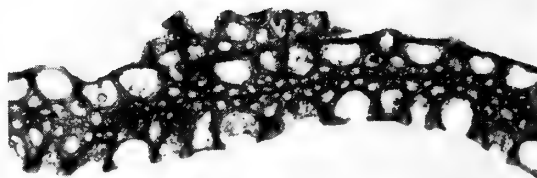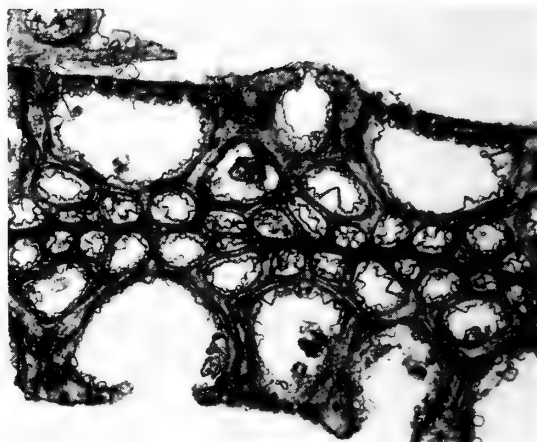
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Figs 26–28 *Elea lamellosa* (d'Orbigny, 1850), photomicrographs of
thin sections of specimens from the Coniacian [?Santonian] of
Villedieu, Loir-et-Cher, France. 26–27, USNM 2737–2; 26,
transverse section, × 26; 27, detail showing median budding
lamina and eleozooid (top centre), × 100. 28, USNM 2737–1,
longitudinal section of an autozooid with in-situ operculum, × 97.

Semielea plana d'Orbigny (see Voigt, 1985*b*: pl. 3, fig. 17) is a unilamellar fragment of *Elea lamellosa* with the beginnings of an eruptive overgrowth, and *Semimultelea irregularis* d'Orbigny is the multilamellar base of an *Elea lamellosa* colony. The identity of *Reptelea pulchella* is uncertain. The lectotype (herein designated) of *R. pulchella* is MNHN d'Orbigny Collection 8196, the specimen in a tube labelled by E. Voigt as the type (Voigt photocard 8316). This Senonian specimen consists of a small colony encrusting a bivalve shell fragment. Eleozooids are lacking. It may be a young stage of *E. lamellosa* or perhaps the base of another meliceritid species.

Semimultelea gradata d'Orbigny is represented by two specimens registered as 8202 in the d'Orbigny Collection, MNHN. One of the specimens is from Tours and appears to be the basal part of a colony of *Elea lamellosa*. The second specimen, from Meudon (Campanian), labelled by E. Voigt as the type (Voigt photocard 5747), is herein designated as the lectotype. This is probably the base of an indeterminate erect meliceritid, and is unlikely to be *Elea lamellosa* in view of the otherwise absence of this species in the chalky facies of Meudon.

Semimultelea irregularis d'Orbigny was selected as the type species of *Semimultelea* d'Orbigny by Gregory (1899: p. 296). Unfortunately, Gregory's material of supposed *S. irregularis* is a mixture of indeterminate Turonian meliceritids with overgrowths, none of them conspecific with true *S. irregularis* (= *Elea lamellosa*). Nevertheless, the type species selection should stand, making the genus *Semimultelea* an objective junior synonym of *Elea*.

DISTRIBUTION. ?Turonian, Coniacian-Santonian of the Loire region and Aquitaine, France. The Turonian record is based on an old specimen (BMNH D11786) and, especially in view of correlation problems, should be regarded as doubtful.

Elea elegantula sp. nov.   Figs 29–43

1985*a*   *Elea* sp. Taylor, fig. 2H and I.

MATERIAL. Holotype: VH 10451, Lower Cenomanian, Mülheim/Ruhr, Germany. Paratypes: VH 9847–8, 10452, 10473, same horizon and locality as paratype. Other material: numerous un-numbered VH topotype specimens.

NAME. With reference to its elegant appearance.

DESCRIPTION. Colony bifoliate with apparently short branches, generally narrow basally and expanded distally, ranging from about 0·7–4 mm in width but typically about 1·6 mm wide, and approximately 0·4 mm deep, often divided distally and frequently twisted. Zooid arrangement varies from regular quincunx to poorly-defined transverse rows, zooids close to the branch margin slightly divergent; organization of all polymorphs fixed-walled. Overgrowths (Fig. 33) may arise through eruptive budding onto branch surface; pseudoancestrula operculate, frontal wall negligable; zone of secondary astogenetic change characterized by autozooids with smaller and more rounded apertures than those in zones of astogenetic repetition. Colony base (Figs 37–38) extensive, giving rise to multiple erect branches whose budding laminae are orientated parallel to local orientation of basal zooids. Ancestrula not observed.

Autozooids (Fig. 29) of moderate size, with pseudoporous frontal walls occupying half or more of the frontal area, about 2 × longer than wide, generally elongate hexagonal in shape with rounded distal borders; zooecial boundaries raised and well-defined. Apertures (Fig. 30) small, longitudinally elongate, up to 1·3 × longer than wide, attaining maximum width a little distal of the hinge line, rounded distally; apertural shelf well-developed, broadening distally; hinge line with a median ridge; apertural rim prominent. Opercula (Fig. 34) frequently preserved in-situ, surface moderately convex, a flattened median proximal area often evident, bearing about 25 elongate pseudopores in a crescent close to the lateral/distal edge. Autozooids and more commonly small eleozooids (Fig. 31) may be budded intramurally within autozooids. Terminal diaphragms, located below level of apertural shelf, very occasionally present.

Eleozooids (Figs 29, 39–40) abundant, most positioned close to branch margins, especially in the recesses of branch divisions, small examples often associated with occluded growing edges. Frontal walls generally a little narrower than those of autozooids, with a similar concentration of pseudopores. Apertures variable in length, most are long, about 3 × longer than wide, tapering distally with concave lateral edges and a well-developed shelf-like rostrum (typical rostrozooids), but these grade into others which are short and subtriangular; maximum apertural width attained at hinge line level. Opercula not observed. Intramural budding of small eleozooids within large eleozooids (Fig. 40) is common, the rostrum being infilled by pseudoporous exterior wall.

Kenozooids of varying size and shape common, mainly located at occluded growing edges, in recesses of branch divisions and in encrusting bases.

Gonozooids (Figs 41–43) common, sometimes more than one per branch fragment. Distal frontal wall emerging from maternal aperture initially parallel-sided, often for a considerable distance, before becoming densely pseudoporous, bulbous and longitudinally ovoidal in shape. Ooeciopore positioned beyond inflated part of frontal wall, transversely elliptical, about one-and-a-half times as wide as long, an internal hemiseptum indenting the proximal edge to give a kidney-shaped deep outline. Atrial ring present in at least some gonozooids.

MEASUREMENTS.

*autozooids* (10 zooids with in-situ opercula from holotype VH 10451)

frontal length:	mean = 0·46 mm; SD = 0·026 mm; CV = 5·5; range = 0·42–0·51 mm
frontal width:	mean = 0·23 mm; SD = 0·008 mm; CV = 3·4; range = 0·23–0·24 mm
apertural length:	mean = 0·17 mm; SD = 0·010 mm; CV = 6·1; range = 0·17–0·20 mm
apertural width:	mean = 0·15 mm; SD = 0·009 mm; CV = 6·5; range = 0·14–0·17 mm

*eleozooids* (10 zooids from holotype VH 10451)

frontal length:	mean = 0·60 mm; SD = 0·139 mm; CV = 23·1; range = 0·32–0·74 mm
frontal width:	mean = 0·20 mm; SD = 0·020 mm; CV = 10·0; range = 0·17–0·23 mm
apertural length:	mean = 0·32 mm; SD = 0·092 mm; CV = 29·3; range = 0·12–0·41 mm
apertural width:	mean = 0·09 mm; SD = 0·012 mm; CV = 12·7; range = 0·08–0·11 mm

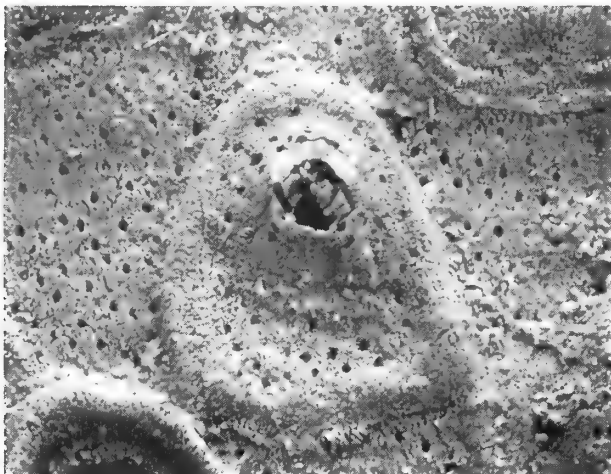*gonozooids* (10 zooids from holotype VH 10451 and un-numbered VH specimens)

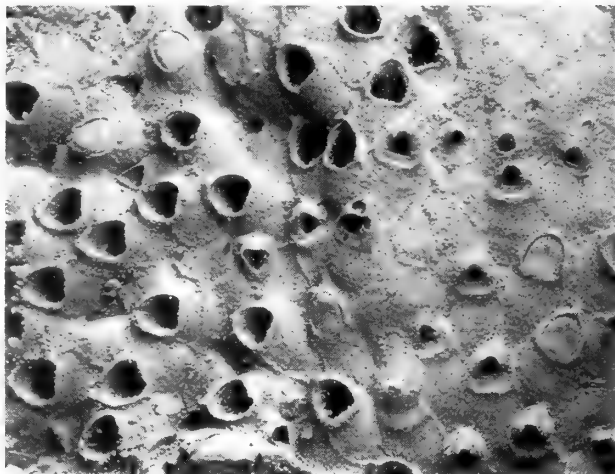|	
frontal length:	mean = 1·69 mm; SD = 0·227 mm; CV = 13·4; range = 1·29–2·03 mm
dilated frontal length*:	mean = 1·06 mm; SD = 0·162 mm; CV = 15·2; range = 0·74–1·31 mm
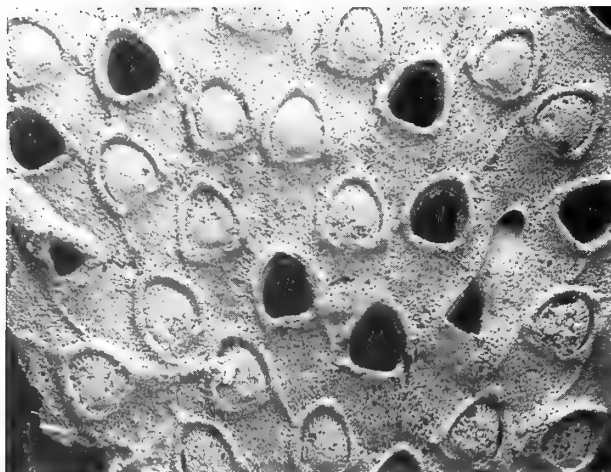
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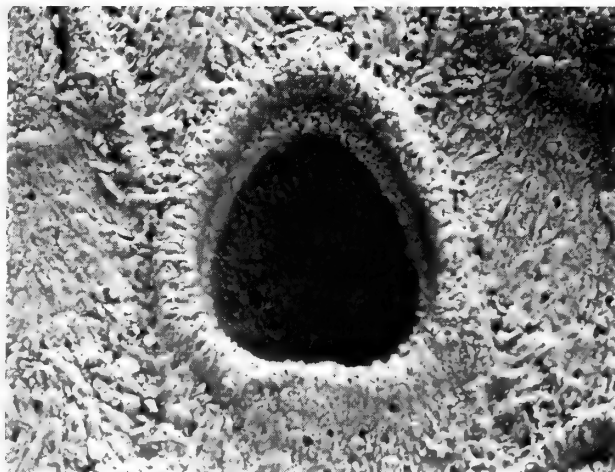
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Figs 29–32 *Elea elegantula* sp. nov., Lower Cenomanian, Mülheim/Ruhr, Germany. 29–30, VH 10451, holotype; 29, autozooids (some with opercula) and eleozooids, × 60; 30, autozooidal aperture, × 250. 31, VH 10452, small intramural eleozooid with partially preserved operculum, × 250. 32, VH 10473, autozooids, small primary eleozooids, intramural eleozooids and kenozooids in encrusting colony base, × 42.

frontal wall width: mean = 0·83 mm; SD = 0·134 mm; CV = 16·2; range = 0·63–1·01 mm
ooeciopore length: mean = 0·08 mm; SD = 0·011 mm; CV = 12·8; range = 0·06–0·09 mm
ooeciopore width: mean = 0·14 mm; SD = 0·019 mm; CV = 13·2; range = 0·12–0·18 mm

(* i.e. that part of the frontal wall beyond the narrow, tubular proximal frontal wall)

REMARKS. Particularly characteristic of this species are the long and narrow eleozooidal apertures and the thick autozooidal apertural rims. *E. elegantula* resembles *E. hexagona* d'Orbigny, 1853, from the Santonian but lacks the tubercle developed distally of the autozooidal aperture, and has frontal walls which occupy a larger proportion of the autozooidal frontal area. It is also very similar to the late Cenomanian/Turonian species *E. subhexagona* sp. nov. but has somewhat smaller zooids with relatively more extensive frontal walls. *E. mackinneyi* sp. nov., which occurs with *E. elegantula* at Mülheim/Ruhr, differs in having broad eleozooidal apertures and more rounded autozooidal apertures.

DISTRIBUTION. Lower Cenomanian of Mülheim/Ruhr, Germany.

Elea flabellata sp. nov.　　　　　Figs 44–48

MATERIAL. Holotype: VH 10448, Lower Santonian, Grube Lengede-Broistedt, near Braunschweig, Germany. Other material: VH unnumbered, 3 abraded fragments from the same horizon and locality probably belong to this species.

NAME. Flabellum, fan (L.), with reference to the flabellate shape of the holotype colony.

DESCRIPTION. Colony bifoliate, consisting in the holotype of a single non-bifurcating, flabellate branch, 3·2 mm wide proximally, expanding to a width of 14 mm distally, about 1·5 mm thick, distinctly elliptical in cross-section at the proximal fracture. Autozooids arranged in approximate quincunx; organization fixed-walled. Colony base and overgrowths not observed.

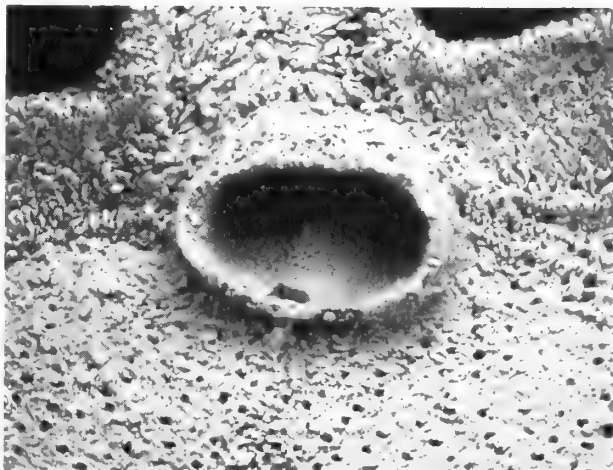Autozooids (Figs 44–45) of small size, frontally a little less
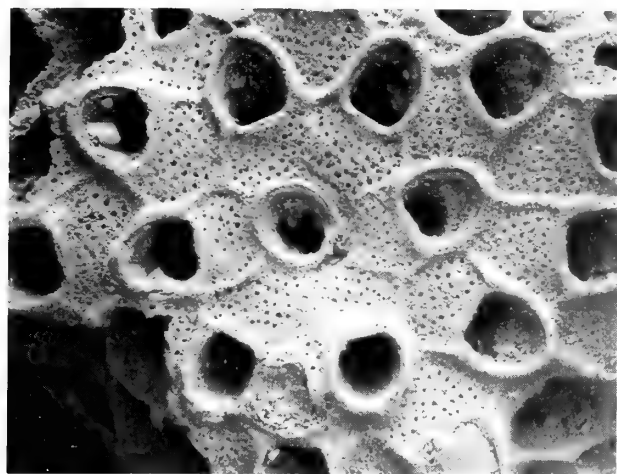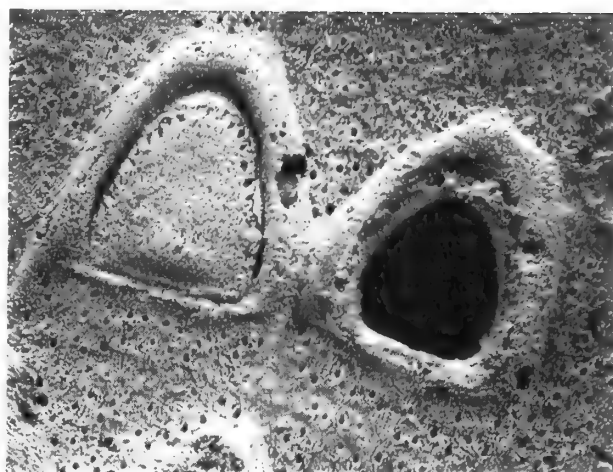
Figs 33–36 *Elea elegantula* sp. nov., Lower Cenomanian, Mülheim/Ruhr, Germany. 33, VH 10452, overgrowth origin, × 85. 34, VH 9848, operculate autozooid (left) and autozooid containing intramural autozooid (right), × 115. 35, VH 9847, proximal part of a gonozooid showing tubular frontal wall emerging from an autozooid-like aperture, × 75. 36, VH 10451, ooeciopore, × 245.

than twice as long as wide and typically hexagonal in outline shape; zooidal boundaries marked by a broad raised area of calcification prolonged into low, blunt tubercles at the corners of zooids; frontal wall pseudoporous, occupying a very small proportion of the frontal surface (Fig. 47), considerably smaller than the autozooidal apertures. Apertures (Fig. 47) medium-sized, slightly longitudinally elongate or equidimensional, attaining maximum width at about mid-length, well-rounded distally; apertural shelf narrow; hinge line with a median bar. Opercula (Fig. 46) occasionally preserved in-situ, surface convex; pseudopores radially elongate, present over entire surface of operculum. Terminal diaphragms not observed. Intramurally budded autozooids (Fig. 45) infrequent, equipped with a thin, raised secondary apertural rim.

Eleozooids (Fig. 48) abundant, scattered, not concentrated at branch margins, frontally on average 1·8 × longer than wide and about 1·5 × the size of an autozooid; frontal wall pseudoporous, occupying a small proportion of the frontal surface but larger than an autozooidal frontal wall. Aperture moderately elongate, about 1·5 × longer than wide, widest at the hinge line, tapering distally to form a narrow, parallel-

sided rostrum which is approximately half the total length of the aperture, rounded distally. Opercula observed in-situ. Intramurally budded autozooids possibly present but rare; intramural eleozooids common, many with apertures facing proximally in a plane oblique to that of the host aperture.

Gonozooids represented by a single example which is both abraded and incompletely formed; longitudinally elongate in outline; ooeciopore and atrial ring not observed.

REMARKS. Only a single adequately-preserved fragment is known of this species. However, the specimen is sufficiently different from other species of *Elea* to be confident that it represents a new species. Although the eleozooids of *E. flabellata* are similar to those present in several other species of *Elea* (e.g. *E. labyrinthica* (Michelin) and *E. hexagona* d'Orbigny), the thick tuberculate calcification which surrounds these as well as the autozooids is very characteristic of the species, as are the much reduced frontal walls. The distribution of pseudopores over the entire surface of the autozooidal operculum is a feature apparently unique to *E. flabellata* among species of *Elea*, although it is present in some species of *Meliceritites* (notably *M. dollfusi* Pergens)
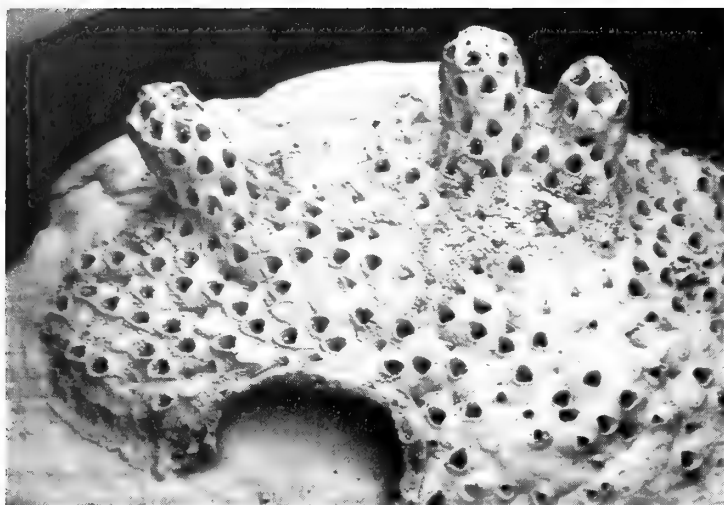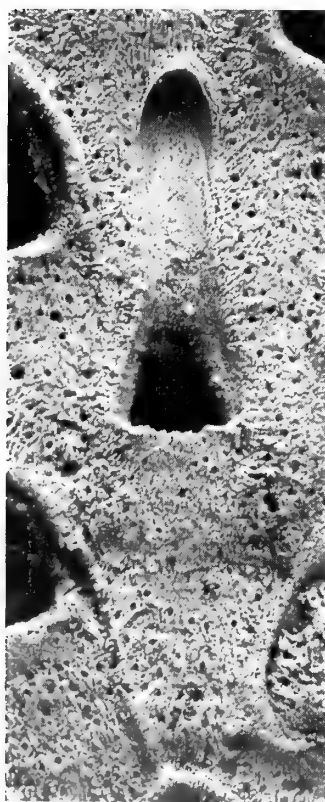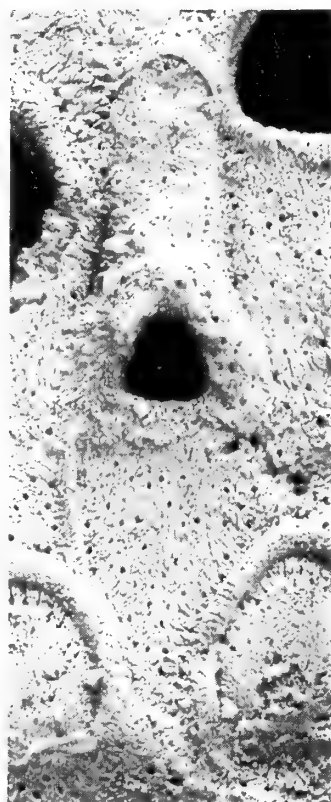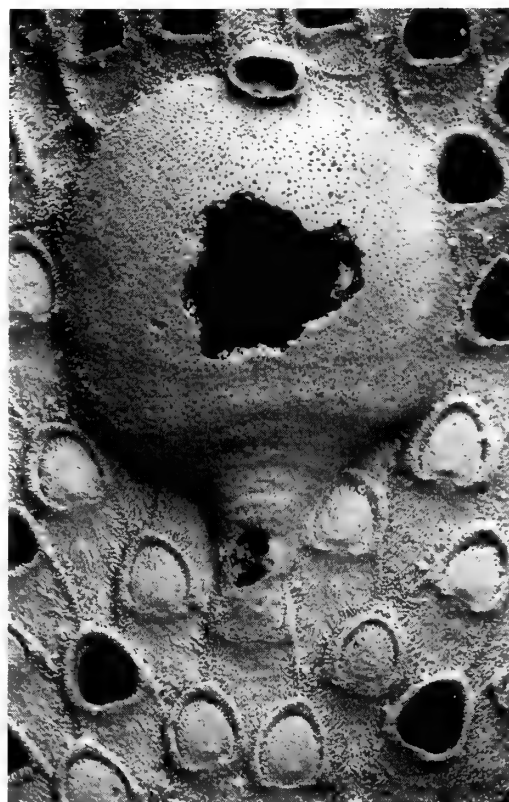
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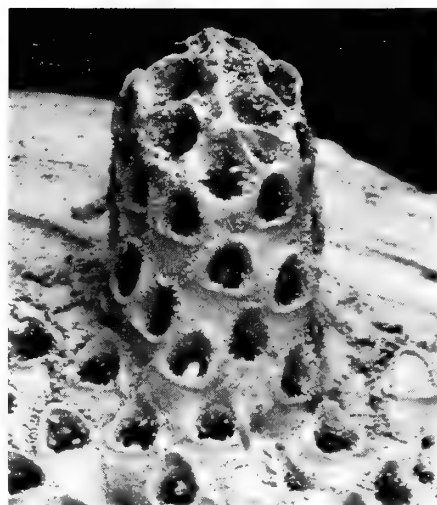
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Figs 37, 38   *Elea elegantula* sp. nov., VH 10473, Lower Cenomanian, Mülheim/Ruhr, Germany; 37, colony base encrusting a shell, giving rise to three erect branches (upper left and right) and forming an arch (lower centre) probably where a soft-bodied organism was overgrown, × 17; 38, base of erect branch, × 50.

39

40

41

Figs 39–41   *Elea elegantula* sp. nov., VH 10451, Lower Cenomanian, Mülheim/Ruhr, Germany; 39, large eleozooid, × 160; 40, large eleozooid containing small intramural eleozooid, × 145; 41, gonozooid with broken roof, × 65.

and in *Reptomultelea scanica* sp. nov. *E. flabellata* bears a resemblance to *Biforicula nodulifera* (Voigt), also from the Santonian of West Germany. Abraded examples of these two species could be difficult to tell apart were it not for the rather more pointed apertures of *B. nodulifera*.

DISTRIBUTION. Lower Santonian of Broistedt, Germany.

MEASUREMENTS.
autozooids (10 zooids with in-situ opercula from holotype VH 10448)

42

43

Figs 42, 43 *Elea elegantula* sp. nov., Lower Cenomanian, Mülheim/Ruhr, Germany 42, VH 10451, inflated frontal wall of gonozooid emerging from an autozooid-like aperture, × 145. 43, VH 10452, gonozooid at the edge of a branch which was apparently aborted after growing the proximal part of the inflated frontal wall; zooids which would have formed the floor of the gonozooid are sealed by exterior walls, × 80.

frontal length:	mean = 0·41 mm; SD = 0·027 mm; CV = 6·7; range = 0·36–0·45 mm
frontal width:	mean = 0·27 mm; SD = 0·015 mm; CV = 5·8; range = 0·24–0·29 mm
apertural length:	mean = 0·21 mm; SD = 0·010 mm; CV = 4·9; range = 0·20–0·23 mm
apertural width:	mean = 0·20 mm; SD = 0·007 mm; CV = 3·6; range = 0·20–0·21 mm

eleozooids (10 zooids from holotype VH 10448)

frontal length:	mean = 0·66 mm; SD = 0·048 mm; CV = 7·3; range = 0·57–0·75 mm
frontal width:	mean = 0·36 mm; SD = 0·020 mm; CV = 5·5; range = 0·35–0·39 mm
apertural length:	mean = 0·40 mm; SD = 0·042 mm; CV = 10·5; range = 0·33–0·45 mm
apertural width:	mean = 0·27 mm; SD = 0·018 mm; CV = 6·6; range = 0·26–0·30 mm

gonozooid (abraded, incomplete zooid from holotype VH 10448)

| total frontal length: | >1·73 mm |
| frontal width: | ca 1·28 mm |

Elea hexagona d'Orbigny, 1853　　　Figs 49–56

1853　*Elea hexagona* d'Orbigny: 633, pl. 738, figs 1–4.
1889　*Elea hexagona* d'Orbigny; Pergens: 398.

non 1897 *b*　*Elea hexagona* d'Orbigny; Canu: 753.
1899　*Elea hexagona* (d'Orbigny); Gregory: 303.
1912　*Meliceritites hexagona* (d'Orbigny); Levinsen: 43, pl. 5, figs 3–5.

MATERIAL. Lectotype (herein designated): MNHN d'Orbigny Collection 8192 (Fig. 49), fragment in tube labelled 'Type' by E. Voigt (Voigt photocard 5791), Senonian [Santonian], Vendôme, Loir-et-Cher, France. Paralectotype: one of the two other fragments registered with lectotype as MNHN 8192 (the third fragment is ?*Foricula*). Other material: ZMC Levinsen Colln M38 and M39, Santonian, Vendôme, France; ZMC Levinsen Colln, about ten un-numbered topotypes.

DESCRIPTION. Colony bifoliate with branches (Figs 49–50) bifurcating, strap-like, narrow, about 1·7–2·3 mm wide. Autozooids usually arranged in approximate quincunx; organization fixed-walled. Colony base not observed. Overgrowths produced by eruptive budding onto the branch surface present.

Autozooids (Fig. 51) moderately large; frontal surface usually hexagonal with edges parallel to long axis or diamond-shaped, elongate, about twice as long as wide; frontal wall small in area, with subcircular pseudopores; zooecial boundaries formed mainly by apertural rims, raised. Apertures (Fig. 52) medium-sized, longitudinally elongate, about 1·2 × longer than wide, attaining maximum width
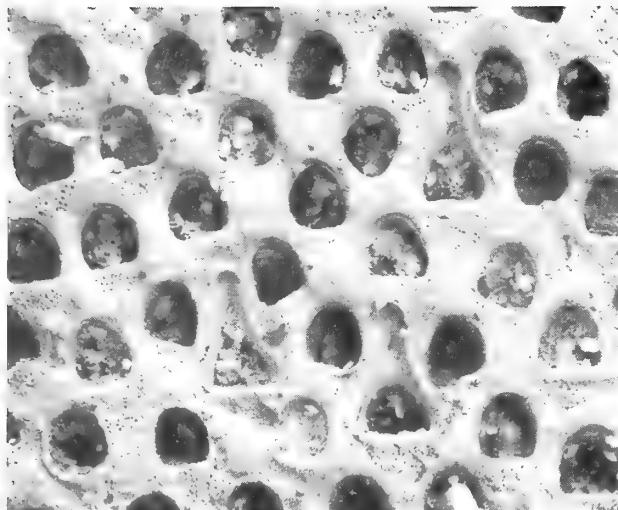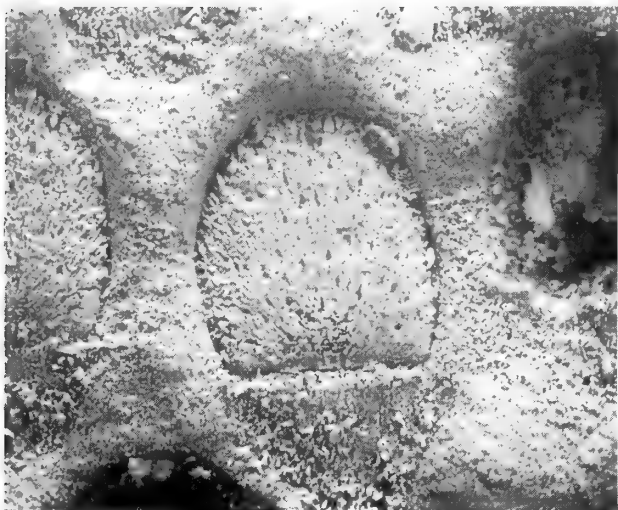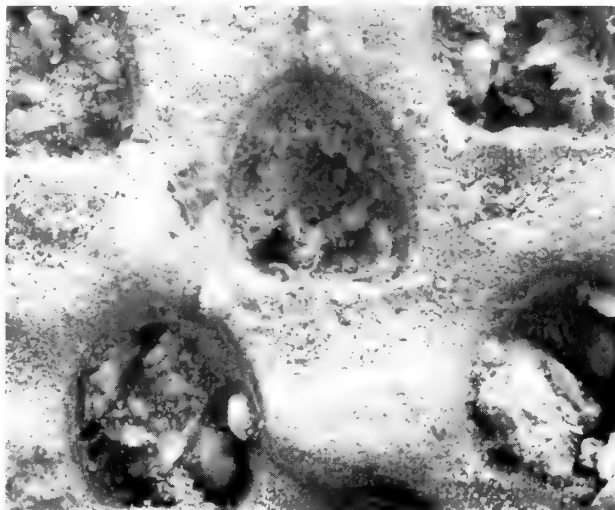
Figs 44–47 *Elea flabellata* sp. nov., VH 10448, holotype, Lower Santonian, Grube Lengede-Broistedt, near Braunschweig, Germany; 44, autozooids and three eleozooids, × 50; 45, autozooids, an eleozooid, and an intramural autozooid (top centre left), × 70; 46, autozooidal operculum, × 200; 47, autozooidal aperture and reduced frontal wall, × 160.

between hinge line and mid-length, rounded distally; apertural shelf variably developed; apertural rim moderately prominent proximally, distally forming a conspicuous, deep tubercle; hinge line bowed. Opercula (Fig. 56) often preserved in-situ, surface convex, pseudopores not evident in poorly-preserved available material. Terminal diaphragms not observed. Intramurally budded autozooids (Figs 52–53) common, some having apertures in same plane as host aperture but significantly smaller and more rounded distally, others having apertures in an oblique plane facing proximally relative to branch orientation and possessing a very prominent tubercle distal to the aperture.

Eleozooids (Figs 51, 53–54) abundant, located particularly at branch margins and in bifurcations, about 2·5–3 × longer than wide, frontally slightly wider and significantly longer than autozooids. Aperture elongate, about 2–2·5 × longer than wide, attaining maximum width at the hinge line and tapering distally to a long, narrow rostrum with a rounded end. Opercula not observed in-situ.

Gonozooid unknown.

MEASUREMENTS (estimated from SEM micrographs).
autozooids

frontal wall length:	*ca* 0·43–0·50 mm
frontal wall width:	*ca* 0·22–0·26 mm
apertural length:	*ca* 0·18–0·21 mm
apertural width:	*ca* 0·16–0·18 mm

eleozooids

frontal wall length:	*ca* 0·62–0·83 mm
frontal wall width:	*ca* 0·25–0·27 mm
apertural length:	*ca* 0·36–0·50 mm
apertural width:	*ca* 0·17–0·23 mm

REMARKS. The supposed *Elea hexagona* described by Canu (1897*b*) from the Cenomanian of Saint-Calais is here included in *E. subhexagona* sp. nov. This species more closely resembles *E. hexagona* than any other species of *Elea* but lacks the very deep and prominent tubercle distal to the

Fig. 48 *Elea flabellata* sp. nov., VH 10448, holotype, Lower Santonian, Grube Lengede-Broistedt, near Braunschweig, Germany; eleozooid, × 185.

Fig. 49 *Elea hexagona* d'Orbigny, 1853, photograph of MNHN d'Orbigny Collection 8192 (Voigt photocard 5791), lectotype, Senonian [Santonian], Vendôme, Loir-et-Cher, France; colony is fouled by serpulids and an oyster; × 10.

autozooidal aperture, which is a characteristic feature of *E. hexagona*. The larger size of the autozooidal apertures enables distinction between *E. hexagona* and *E. labyrinthica*. Filliozat (1908) records *E. hexagona* from the Calcaire graveleux, Assise á *Crania ignabergensis*, Craie de Vendôme. Unfortunately, the species is unrepresented in both the BMNH and VH collections.

DISTRIBUTION. Santonian of Vendôme, Loir-et-Cher, France.

Elea labyrinthica (Michelin, 1843)   Figs 57–65

1843   *Eschara labyrinthica* Michelin: 124, pl. 32, fig. 2.
1843   *Eschara neustriaca* Michelin: 124, pl. 32, fig. 3.
1853   *Elea rhomboidalis* d'Orbigny: 631, pl. 737, figs 21–24.
1890   *Elea rhomboidalis* d'Orbigny; Pergens: 399.
1899   *Elea labyrinthica* (Michelin); Gregory: 303.
1899   *Elea rhomboidalis* d'Orbigny; Gregory: 304.

MATERIAL. Type: the syntypes of this species (and of the contemporaneous *Eschara neustriaca*) are not among the Michelin types in the MNHN (see Walter 1975); Michelin (1843) gives Cap de la Hève, Honfleur, Villers-sur-Mer and Vaches-Noires as localities, and Craie Chloritée [= Craie Glauconieuse, Lower Cenomanian] as the horizon. Other material: MNHN d'Orbigny Collection 6627 [= Voigt photo-card 7475] (presumed type specimen of *E. rhomboidalis*), Cenomanian, Le Havre, France; BMNH D31139, VH 10460, Cenomanian, Cap de la Hève, Seine Maritime, France; BMNH D58900–2, Lower Cenomanian, Craie Glauconieuse, Cap de la Hève; BMNH D58763–4, D58890–2, Craie Glauconieuse, Port d'Antifer, Seine Maritime, France; BMNH D59156 (sample), Craie Glauconieuse, Villers-sur-Mer, Calvados, France; BGS GSM 118097-8, Lower Cenomanian, Warminster Greensand, Warminster, Wiltshire, England, Cunnington Collection; BGS GSM Rh 4582, Cenomanian Limestone, ?Bed A1, Hall Rocks to Beer Head, Devon, England; BMNH D59157, Cenomanian Limestone, Bed A1 (*mantelli* Zone), The Pinnacles, near Beer, Devon; BMNH D59158, Cenomanian (float), White Hart Sandpit, Wilmington, Devon. VH unnumbered specimens, Lower Cenomanian (*carcitanensis* Zone), Carriére du Billot, Notre-Dame-de-Fresnaye, Calvados, collected by G. Breton.

DESCRIPTION. Colony bifoliate with branches of variable morphology, strap-like, bifurcating and about 6 mm wide in some specimens, broad and folded in others (e.g. Michelin 1843, pl. 32, fig. 2); branches about 0·9 mm deep. Zooids arranged in regular to approximate quincunx (Figs 57, 61); organization fixed-walled. Overgrowths extremely common, originating through eruptive budding onto the surfaces of erect branches; growing edges of overgrowths sometimes closed by terminal diaphragms. Colony base extensive, giving rise to more than one erect branch. Possible conspecific ancestrula adjacent to a gonozooid in VH 10460 has a very short distal tube and large protoecium about 0·22 mm wide.

Autozooids (Figs 57, 61–62) medium-sized, with frontal walls elongate, over twice as long as wide, typically hexagonal but occasionally diamond-shaped, pierced by circular to
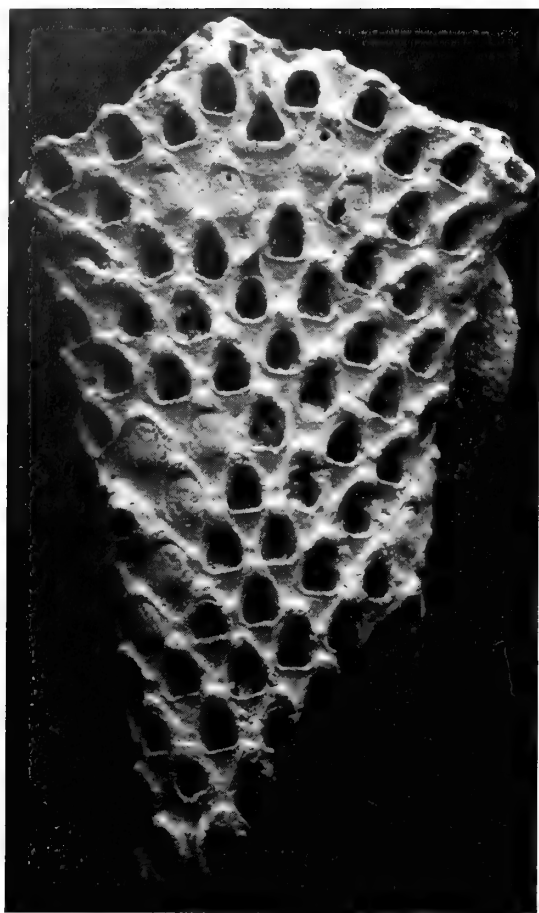
Fig. 50 *Elea hexagona* d'Orbigny, 1853, ZMC Levinsen Collection M39, Santonian, Vendôme, France, × 28.

slightly longitudinally elongate pseudopores; zooidal boundaries marked by low, thread-like ridges. Apertures (Fig. 59) small, longitudinally elongate, a little less than 1·5 × longer than wide, attaining maximum width about mid-length, rounded distally; apertural shelf distinct, narrow; hinge line very slightly bowed, teeth not clearly apparent; apertural rim raised. A large and prominent tubercle (Fig. 61) occurs distally of the autozooidal aperture and is shaped like a compressed barkhan dune facing towards the aperture. Opercula (Fig. 58) fairly commonly found in-situ, surface convex, bearing about 10 radial ridges peripheral to a central flatter area; pseudopores not seen. Intramural eleozooids often present; apertures variably D-shaped to inverted T-shaped, located within the distal half of the aperture of the host autozooid. Intramural autozooids possibly present but infrequent.

Eleozooids (Figs 57, 60, 62–64) common, scattered or in small groups, with pseudoporous frontal walls having approximately the same area as, though often narrower than, those of autozooids. Apertures highly variable in length, ranging from about 2 to 5 × longer than wide, tapering to become very narrow at the rounded distal extremity; apertural shelf wide, beginning just distally of the hinge-line; distal tubercle absent. Opercula (Fig. 63) occasionally found in-situ. Intramural eleozooids (Fig. 64) often present.

Gonozooids known from only one specimen (VH 10460), which has an intact and an abraded example; in the former (Fig. 65) an initially narrow, tubular distal frontal wall becomes densely pseudoporous before dilating into an elongate ovoid shape. Ooeciopore circular or slightly longitudinally elongate, about the same length as an autozooidal aperture. Atrial ring not apparent in the abraded gonozooid, in which the vertical walls of the more proximally overgrown zooids protrude from the floor of the gonozooid, whereas those of the more distal zooids do not.

MEASUREMENTS.
autozooids
(10 zooids with in-situ opercula from BGS GSM Rh 4582)

frontal length:	mean = 0·55 mm; SD = 0·033 mm; CV = 6·1; range = 0·50–0·60 mm
frontal width:	mean = 0·22 mm; SD = 0·023 mm; CV = 10·2; range = 0·18–0·26 mm
apertural length:	mean = 0·14 mm; SD = 0·014 mm; CV = 10·1; range = 0·12–0·17 mm
apertural width:	mean = 0·10 mm; SD = 0·010 mm; CV = 10·6; range = 0·08–0·11 mm

(10 zooids from BMNH D31139)

frontal length:	mean = 0·58 mm; SD = 0·043 mm; CV = 7·4; range = 0·53–0·63 mm
frontal width:	mean = 0·25 mm; SD = 0·016 mm; CV = 6·3; range = 0·23–0·27 mm
apertural length:	mean = 0·15 mm; SD = 0·007 mm; CV = 4·7; range = 0·14–0·17 mm
apertural width:	mean = 0·11 mm; SD = 0·007 mm; CV = 6·7; range = 0·09–0·12 mm

eleozooids (5 zooids from BGS GSM Rh 4582; 5 zooids from BMNH D31139)

frontal length:	range = 0·42–1·02 mm
frontal width:	range = 0·17–0·27 mm
apertural length:	range = 0·20–0·54 mm
apertural width:	range = 0·06–0·09 mm

gonozooid (VH 10460)

total frontal length:	2·72 mm
distal frontal wall length:	2·51 mm
frontal wall width:	0·98 mm
ooeciopore length:	0·11 mm
ooeciopore width:	0·11 mm

REMARKS. Although type material is lacking, the identity of this species is not in doubt as Michelin's enlarged figure (1843: pl. 32, fig. 2b) shows very clearly the prominent tubercles located distally of the autozooidal apertures. In no other melicerititid species are the distal tubercles so well-developed or shaped so much like barkhan dunes.

Specimens of *E. labyrinthica* from the type horizon – the Craie Glauconieuse, where it is very common, exhibit variable colony forms, some being adeoniform while others are eschariform. One specimen (BMNH D58763) encrusts a sponge.

DISTRIBUTION. Lower Cenomanian of northern France and south-west England; known from sandy facies only.

Elea mackinneyi sp. nov.   Figs 66–71

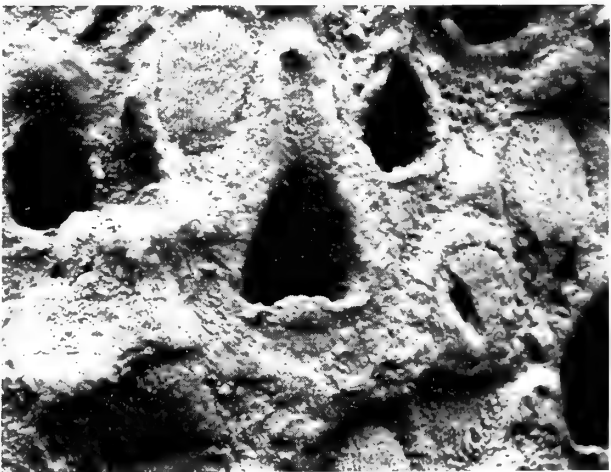MATERIAL. Holotype: VH 10474, Lower Cenomanian, Mülheim/Ruhr, Westfalia, Germany. Paratypes: VH 10541 (4
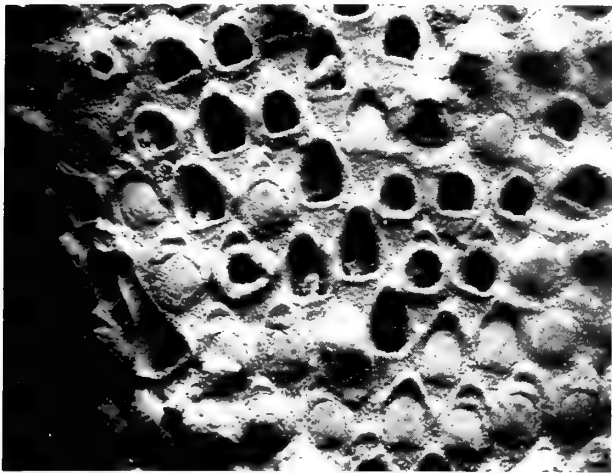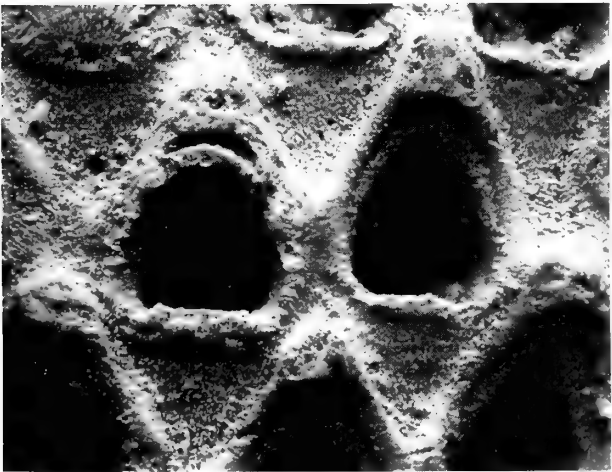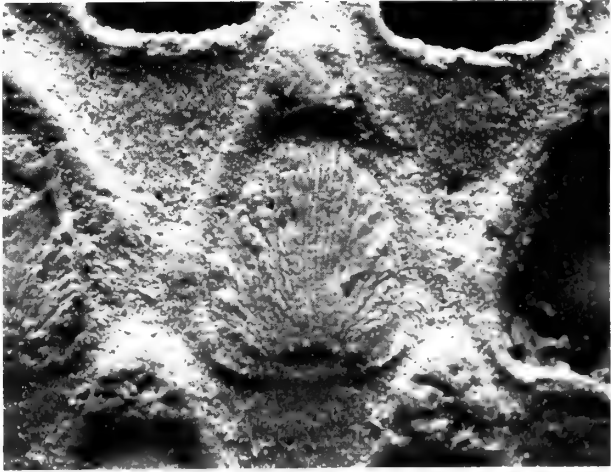
Figs 51–56 *Elea hexagona* d'Orbigny, 1853, Santonian, Vendôme, France. 51–54, ZMC Levinsen Collection M38; 51, autozooids and a marginal eleozooid (lower left), × 33; 52, intramural operculate autozooid (left) and autozooidal aperture (right), × 135; 53, marginal eleozooid and intramural autozooids, × 70; 54, non-marginal eleozooid, × 98. 55, 56, ZMC M39; 55, intramural autozooid (left) and normal autozooid (right), × 135; 56, autozooidal operculum, × 150.
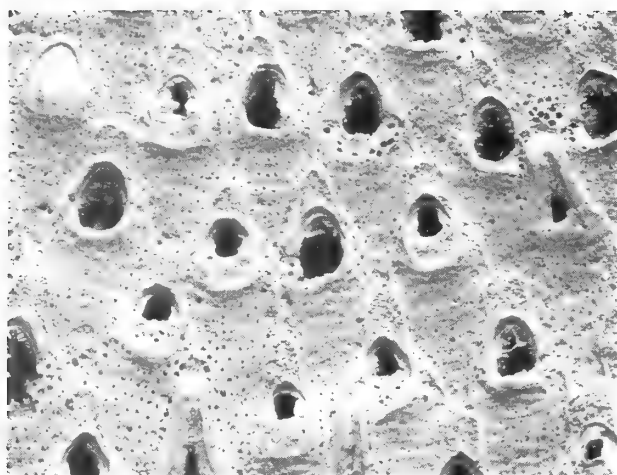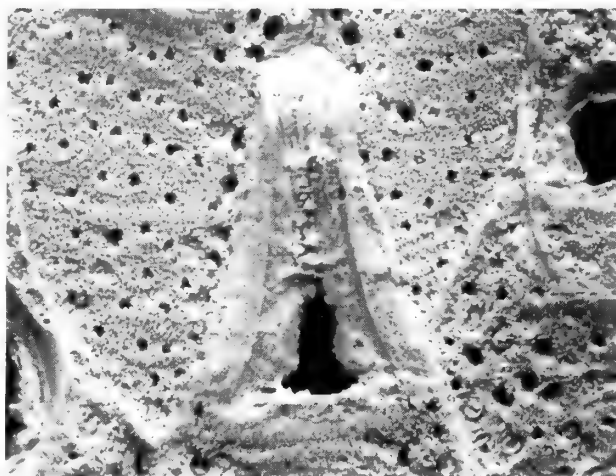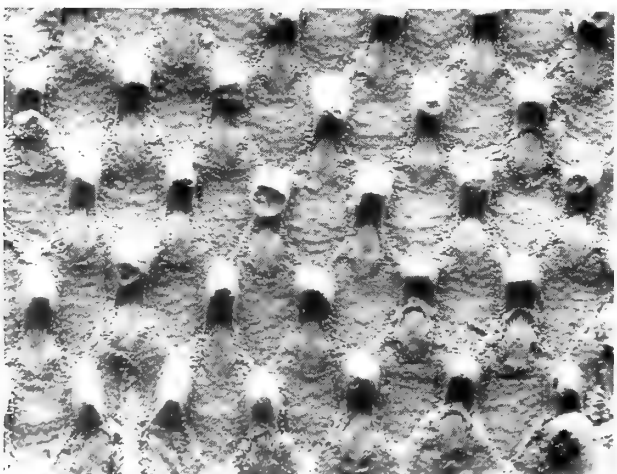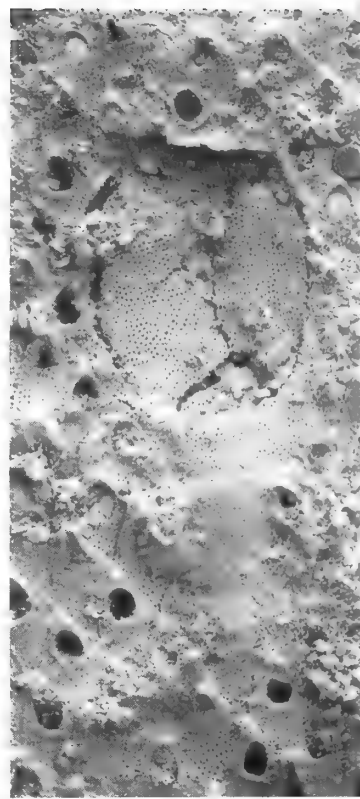
Figs 57–62   *Elea labyrinthica* (Michelin, 1843). 57–60, BMNH D31139, Cenomanian, Cap de la Hève, Seine Maritime, France; 57, autozooids, eleozooids and intramural eleozooids; distal tubercles abraded, × 55; 58, autozooidal operculum, × 170; 59, autozooidal aperture, × 185; 60, eleozooid with distally broken rostrum, × 175. 61, 62, BGS GSM Rh 4582, Cenomanian Limestone, ?Bed A1, Hall Rocks to Beer Head, Devon, England; 61, autozooids with prominent distal tubercles, × 48; 62, autozooids and eleozooids with long, narrow rostra, × 70.

Figs 63–65 *Elea labyrinthica* (Michelin, 1843). 63, 64, BGS GSM Rh 4582, Cenomanian Limestone, ?Bed A1, Hall Rocks to Beer Head, Devon, England; 63, large eleozooid with slightly damaged operculum, × 145; 64, two large eleozooids housing small intramural eleozooids, × 110. 65, VH 10460, Cenomanian, Cap de la Hève, Seine Maritime, France, gonozooid with crushed frontal wall, × 35.

specimens), same horizon and locality as holotype.

NAME. In recognition of the numerous fundamental contributions made to bryozoology by Dr F.K. McKinney (Appalachian State University).

DESCRIPTION. Colony bifoliate with branches (Fig. 66) narrow, strap-like, about 1·8 mm wide between bifurcations, and 0·7 mm deep. Autozooids generally arranged in transverse rows whose regularity is disrupted close to bifurcations; organization fixed-walled. Overgrowths and colony base not observed.

Autozooids (Fig. 67) medium-sized, with elongate hexagonal frontal walls on average slightly less than 2 × longer than wide; pseudopores circular or longitudinally elliptical; zooecial boundaries raised. Apertures small, longitudinally elongate, about 1·1 × longer than wide, attaining maximum width a little proximally to mid-length, appreciably narrower at hinge line level; apertural shelf absent or at most very slightly developed; apertural rim moderately raised; hinge line straight or slightly bowed, typically concave in eroded zooids lacking opercula. Opercula (Fig. 69) rarely preserved in-situ, flat or slightly depressed, bearing about 16 pseudopores arranged in a crescent parallel to the distal/lateral margin. Terminal diaphragms not observed. Intramurally budded autozooids represented by a single example with a slightly oblique aperture (Fig. 70).

Eleozooids (Figs 67, 68) common, located along branch margins, on average about 3 × longer than wide, usually occupying two transverse rows of autozooids. Aperture long, widest at the hinge line but broad throughout, sometimes very slightly spatulate, well-rounded distally, on average twice as long as wide. In-situ opercula and intramural buds not observed.

Kenozooids (Fig. 68) occasionally present at branch margins, especially within bifurcations.

Gonozooids (Fig. 71) of unknown abundance (one fully developed and one partially developed example present in holotype VH 10474); distal frontal wall dilating soon after emerging from maternal aperture, longitudinally ovoidal in shape, about 2 × longer than wide. Ooeciopore not observed. Atrial ring present.

MEASUREMENTS.
autozooids (10 zooids from holotype VH 10474)

frontal length:	mean = 0·49 mm; SD = 0·029 mm; CV = 6·0; range = 0·45–0·54 mm
frontal width:	mean = 0·26 mm; SD = 0·018 mm; CV = 6·7; range = 0·24–0·29 mm
apertural length:	mean = 0·18 mm; SD = 0·006 mm; CV = 3·6; range = 0·17–0·18 mm
apertural width:	mean = 0·16 mm; SD = 0·005 mm; CV = 2·9; range = 0·15–0·17 mm

eleozooids (10 zooids from holotype VH 10474)

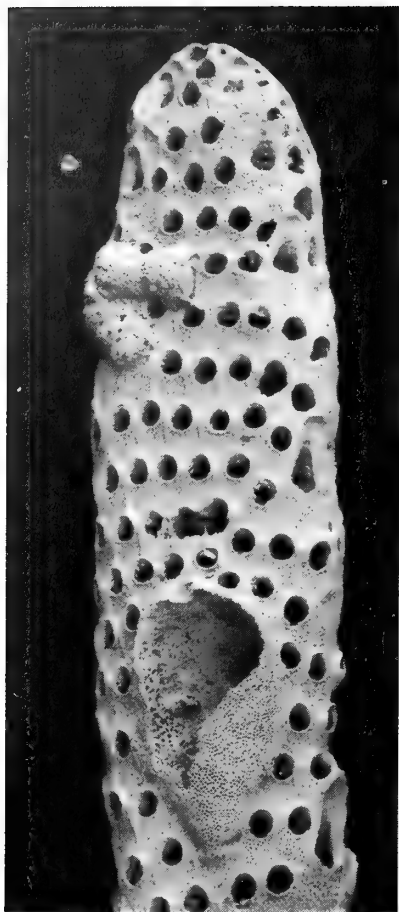|	
frontal length:	mean = 1·00 mm; SD = 0·184 mm; CV = 18·5; range = 0·75–1·26 mm

Fig. 66 *Elea mackinneyi* sp. nov., VH 10474, holotype, Lower Cenomanian, Mülheim/Ruhr, Westfalia, Germany; branch with broken gonozooid and fouling foraminifer (top left), × 20.

frontal width:	mean = 0·36 mm; SD = 0·050 mm; CV = 13·9; range = 0·30–0·44 mm
apertural length:	mean = 0·49 mm; SD = 0·102 mm; CV = 20·7; range = 0·33–0·65 mm
apertural width:	mean = 0·24 mm; SD = 0·034 mm; CV = 13·8; range = 0·18–0·29 mm

gonozooid (from holotype VH 10474)

total frontal length:	2·34 mm
dilated frontal wall length:	2·07 mm
frontal wall width:	1·04 mm

REMARKS. Although known from only a few specimens, this is a very distinctive species. The broad shape of the eleozooid rostra serve to distinguish *Elea mackinneyi* from sympatric *Elea elegantula* sp. nov., and it differs from *E. viskovae* sp. nov. from the Turonian of the Kazakhstan in having longer rostra and in lacking an appreciable autozooidal apertural shelf.

DISTRIBUTION. Lower Cenomanian of Germany.

Elea pseudolamellosa sp. nov.   Figs 72–78

MATERIAL. Holotype: VH 10462, Upper Campanian, St Severin d'Uzel, Charente Maritime, France. Paratypes: VH 10461, same horizon and locality as holotype; VH 10471, Senonian, La gare de Soullans, Vendée, France. BMNH BZ 441–4 , Upper Campanian, Cailleau, near Talmont, Charente Maritime, France. Other material: VH unnumbered topotypes.

NAME. With reference to its similarity to *Elea lamellosa* (d'Orbigny).

DESCRIPTION. Colony bifoliate, consisting of broad, folded fronds about 0·9 mm deep. Growing edge may be occluded by kenozooids and eleozooids. Colony base not observed. Overgrowths may be present. Zooids arranged in approximate quincunx; organization fixed-walled.

Autozooids (Figs 72, 76) medium-sized, frontally hexagonal in outline, on average 1·6 × as long as wide, distal edge prolonged by aperture; frontal wall slightly convex, with circular pseudopores; zooecial boundary wall inconspicuous, thin, little raised. Apertures (Fig. 74) small, longitudinally elongate, about 1·2 × longer than wide, reaching maximum width a little distally of the hinge line, well-rounded distally; apertural shelf narrow; apertural rim narrow but prominent, continuous with zooecial boundary wall; hinge line bowed. Opercula (Fig. 73) infrequently preserved in-situ, prominent, surface convex, seemingly with radially elongate pseudopores widely distributed. Terminal diaphragms not observed. Intramural eleozooids present, their D-shaped apertures occupying the distal part of the host aperture, which is proximally covered by a slightly concave pseudoporous exterior wall.

Eleozooids (Figs 72, 76–77) common, often clustered, especially near occluded growing edges; frontally variable in size, typically only slightly smaller than autozooids; frontal wall with circular pseudopores. Apertures (Fig. 77) small, D-shaped, equidimensional or transversely elongate. In-situ opercula and intramural buds not observed.

Kenozooids observed in association with eleozooids and gonozooids (Fig. 75).

Gonozooids (Fig. 78) large, longitudinally elongate; frontal wall with a short parallel-sided portion emerging from the maternal zooidal aperture (Fig. 75), dilating into an ovoidal distal portion about twice as long as wide. Ooeciopore not observed (destroyed during abrasion of frontal wall in available specimens). Atrial ring not observed.

MEASUREMENTS.

autozooids (10 zooids from holotype VH 10462)

frontal length:	mean = 0·53 mm; SD = 0·029 mm; CV = 5·6; range = 0·48–0·57 mm
frontal width:	mean = 0·33 mm; SD = 0·024 mm; CV = 7·2; range = 0·30–0·38 mm
apertural length:	mean = 0·18 mm; SD = 0·014 mm; CV = 7·7; range = 0·17–0·21 mm
apertural width:	mean = 0·15 mm; SD = 0·007 mm; CV = 4·7; range = 0·14–0·17 mm

eleozooids (estimated from SEM micrographs of VH 10461–2)

apertural length:	*ca* 0·05–0·07 mm
apertural width:	*ca* 0·06–0·07 mm

gonozooid (one zooid from VH 10462)

frontal length:	2·52 mm

67

68

69

70
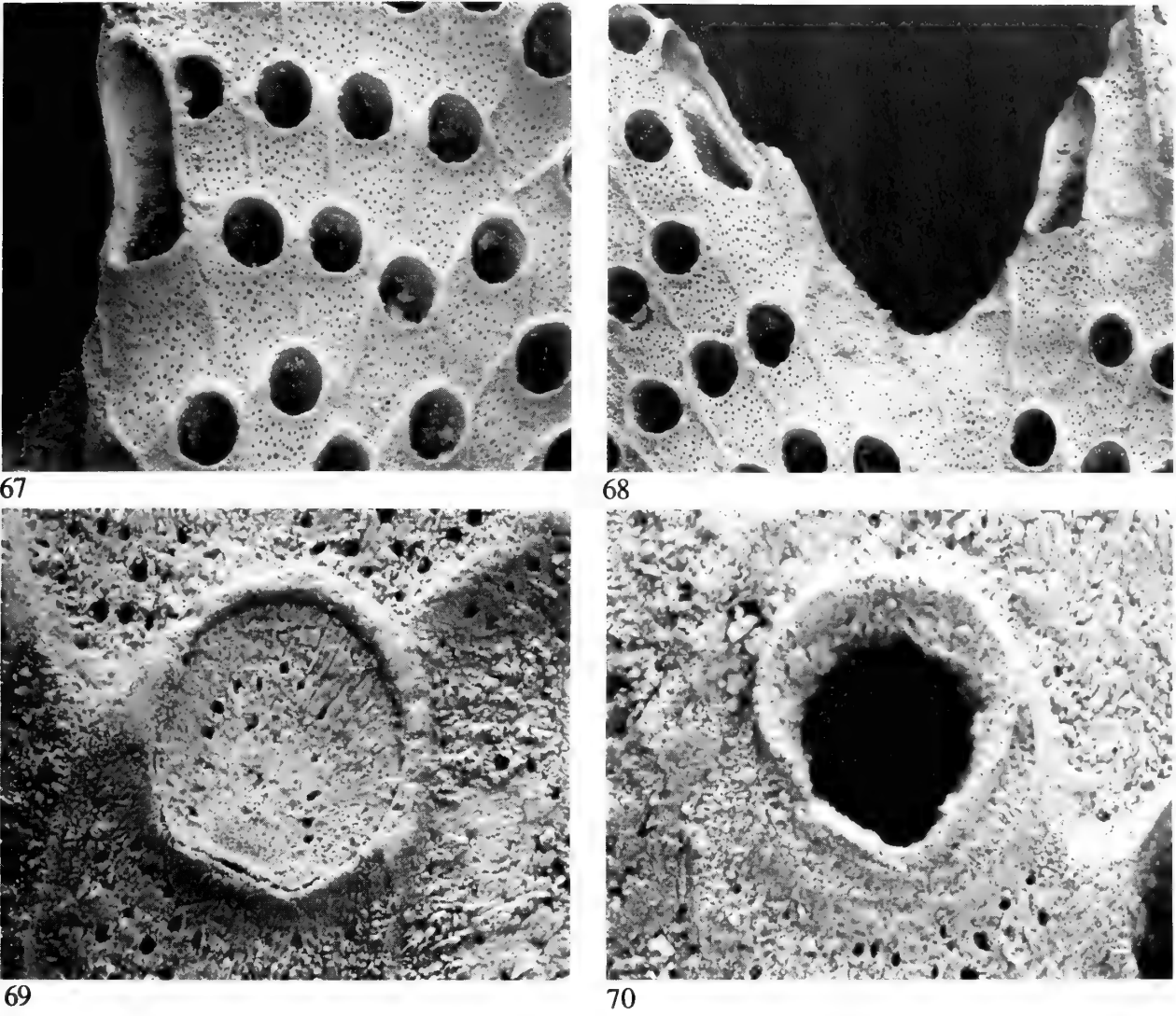
Figs 67–70 *Elea mackinneyi* sp. nov., VH 10474, holotype, Lower Cenomanian, Mülheim/Ruhr, Westfalia, Germany; 67, autozooids and marginal eleozooid, × 55; 68, two marginal eleozooids and kenozooids at a bifurcation, × 44; 69, autozooidal operculum, × 265; 70, oblique intramural autozooidal aperture, × 265.

distal frontal length: 2·31 mm
frontal width: 1·20 mm

REMARKS. This species is extremely similar to *Elea lamellosa* d'Orbigny (see p. 17). The principal point of distinction is the D-shaped form of the eleozooid aperture, which contrasts with the inverted T-shaped aperture characteristic of the eleozooids in *E. lamellosa*. (i.e. the eleozooids of *E. pseudolamellosa* are demizooids, whereas those of *E. lamellosa* are trifoliozooids; compare Figs 77 and 19) This difference appears to reflect the presence of a rostral shelf in *E. lamellosa* which is absent in *E. pseudolamellosa*. Autozooidal frontal walls may be a little more convex and zooecial boundary walls rather less well-developed in *E. pseudolamellosa* than in *E. lamellosa*. The stratigraphical distribution of the two species differs, *E. lamellosa* occurring in the Coniacian-Santonian (and possibly the Turonian), whereas *E. pseudolamellosa* is known with certainty only from the Upper Campanian; a paratype (VH 10471) from the Vendée

assigned to *E. pseudolamellosa* is of unknown age within the Senonian.

DISTRIBUTION. Upper Campanian of Charente Maritime, and undifferentiated Senonian of the Vendée, France.

Elea subhexagona sp. nov.   Figs 79–86

non 1846   *Escharites dichotoma* Reuss: 66, pl. 15, fig. 31.
    1874   *Echarites dichotoma* (Reuss); Reuss: 135, pl. 25, fig. 8.
    1897b   *Elea hexagona* d'Orbigny; Canu: 753.

MATERIAL. Holotype: DM un-numbered, Voigt photocard 2060 (specimen figured by Reuss 1874, pl. 25, fig. 8), Upper Turonian, 'Oberen Pläners', Strehlen, Dresden, Germany. Paratypes: ZMC M53–5, 'Turonien' [probably Cenomanian], St Calais, Sarthe, France. Other material: MNHN Canu Collection unnumbered.
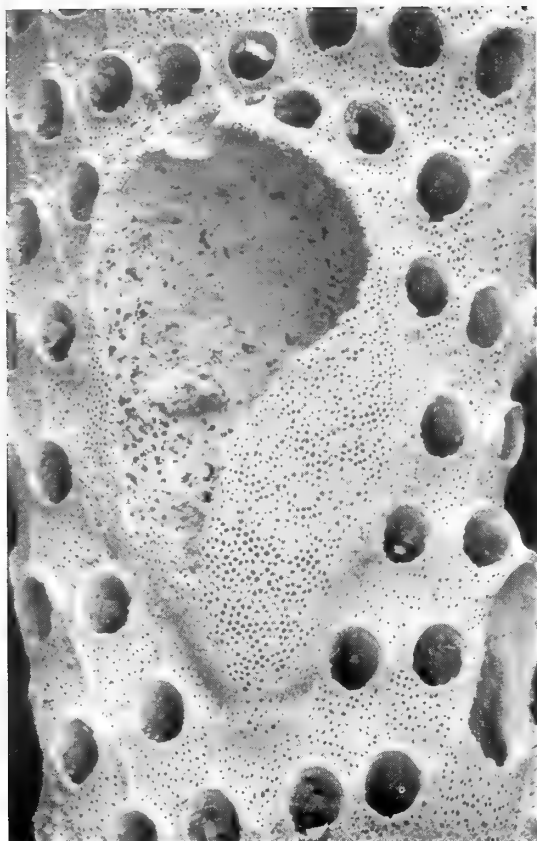
Fig. 71 *Elea mackinneyi* sp. nov., VH 10474, holotype, Lower Cenomanian, Mülheim/Ruhr, Westfalia, Germany; gonozooid with broken frontal wall exposing atrial ring, × 48.

NAME. With reference to the resemblance to *Elea hexagona*.

DESCRIPTION. Colony bifoliate with branches (Fig. 79) bifurcating, strap-like, narrow, about 1·3–2·3 mm wide. Autozooids generally arranged in approximate quincunx; organization fixed-walled. Colony base not observed. Overgrowth present in ZMC M54, consisting of kenozooids spreading between apertures of underlying autozooids, possibly free-walled (Fig. 79).

Autozooids (Figs 80, 81) medium-sized; frontal surface usually hexagonal, elongate, about twice as long as wide; frontal wall occupying about half of frontal surface, flat with circular pseudopores; zooecial boundaries raised. Apertures (Fig. 83) small, longitudinally elongate, on average 1·1–1·2 × longer than wide, attaining maximum width between hinge line and mid-length, rounded distally; apertural shelf narrow; apertural rim well-developed; hinge line with a subdued median bar. Opercula (Fig. 82) often preserved in-situ, surface convex, sometimes with a flattened median area close to the hinge line, pseudopores not visible in studied material. Terminal diaphragms not observed. Intramurally budded autozooids may be present, their apertures typically shorter and more rounded than normal autozooids.

Eleozooids (Figs 84–85) common, especially at branch margins and in bifurcations, about 3–4 × longer than wide, frontally slightly wider but appreciably longer than autozoo-

ids. Aperture elongate, about 2–3 × longer than wide, widest at the hinge line and tapering to a long narrow rostrum with a rounded end. Opercula (Fig. 84) observed in-situ, surface convex. Intramurally budded eleozooids (Fig. 81) present.

Kenozooids sometimes present in branch bifurcations.

Gonozooids (Fig. 86) with a short parallel-sided proximal frontal wall emerging from the maternal zooid aperture, becoming longitudinally ovoidal, distal dilated frontal wall approximately 1·5 × longer than wide. Ooeciopore removed by abrasion; atrial ring present.

MEASUREMENTS.

autozooids (10 zooids with in-situ opercula from the holotype)

frontal length:	mean = 0·53 mm; SD = 0·040 mm; CV = 7·6; range = 0·48–0·60 mm
frontal width:	mean = 0·27 mm; SD = 0·019 mm; CV = 7·1; range = 0·26–0·30 mm
apertural length:	mean = 0·19 mm; SD = 0·007 mm; CV = 4·1; range = 0·18–0·20 mm
apertural width:	mean = 0·17 mm; SD = 0·007 mm; CV = 4·3; range = 0·15–0·18 mm

eleozooids (5 zooids from the holotype)

frontal length:	range = 0·74–0·81 mm
frontal width:	range = 0·23–0·29 mm
apertural length:	range = 0·36–0·42 mm
apertural width:	range = 0·15–0·20 mm

*gonozooids* (2 zooids estimated from SEM micrographs of ZMC M53 and M55)

total frontal length:	ca 1·61–1·88 mm
distal frontal wall length*:	ca 1·24–1·44 mm
frontal width:	ca 0·85–0·96 mm

(* i.e. that part of the frontal wall distal to the narrow origin)

REMARKS. This new species was identified by Reuss (1874) as *Escharites dichotoma* Reuss, 1846. Unfortunately, the type specimen of *E. dichotoma*, from the Exogyrensandstein of Bohemia, was destroyed in 1956 (E. Voigt pers. comm. December 1986). However, it is clear from the figure of Reuss (1846), which depicts a vinculariiform colony resembling *Filicea*, that it is not the same species as *E. dichotoma* sensu Reuss, 1874.

Canu (1897b) identified specimens here regarded as *Elea subhexagona* as *E. hexagona* d'Orbigny, a Santonian species which is very similar to *E. subhexagona* but which can be distinguished by the deep and prominent tubercle situated distally to the autozooidal aperture. Canu apparently realized later that this identification was mistaken because material of his in the MNHN and in the ZMC (donated to G.M.R. Levinsen) is labelled with the MS name 'Elea fissurata'. The exact stratigraphical horizon of these specimens from St Calais (Sarthe) is questionable; Canu originally ascribed his St Calais material to the Cenomanian but subsequently referred it to the Turonian (Canu and Bassler, 1922). It seems possible that the specimens are from the late Cenomanian *plenus* Zone, although *E. subhexagona* is not represented among material of this age from St Calais in the VH and BMNH collections.
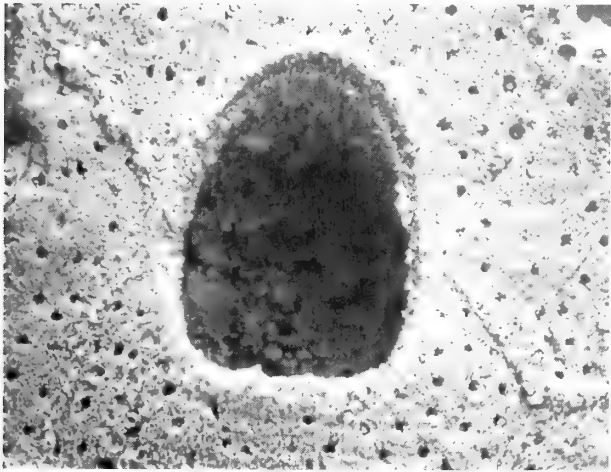
DISTRIBUTION. Upper Cenomanian/Lower Turonian of St Calais, Sarthe, France, and Upper Turonian of Dresden, Germany.
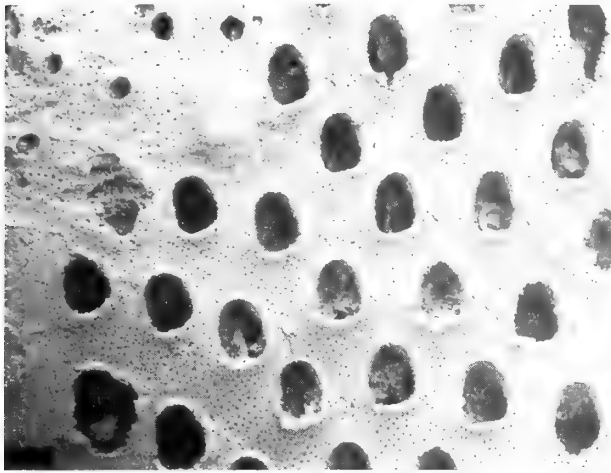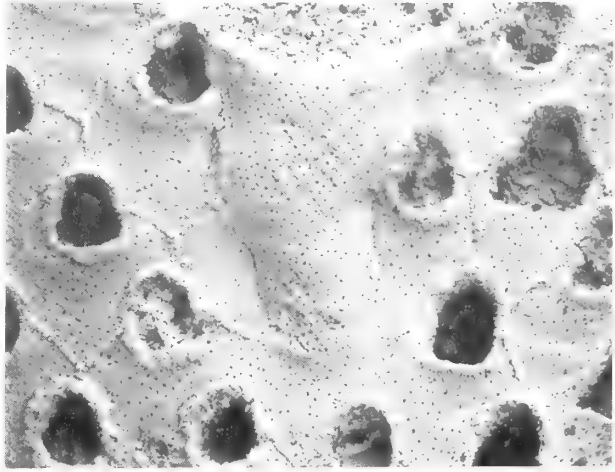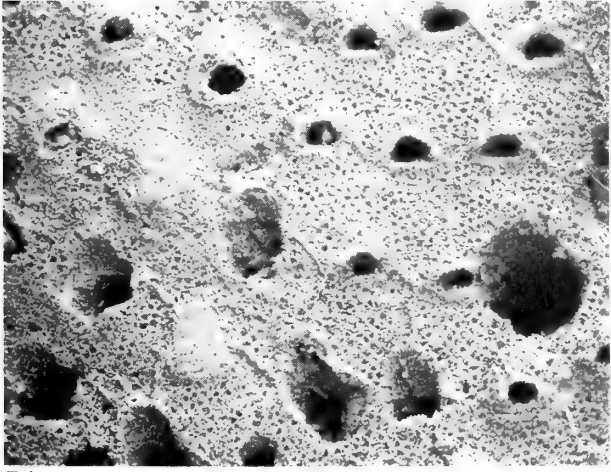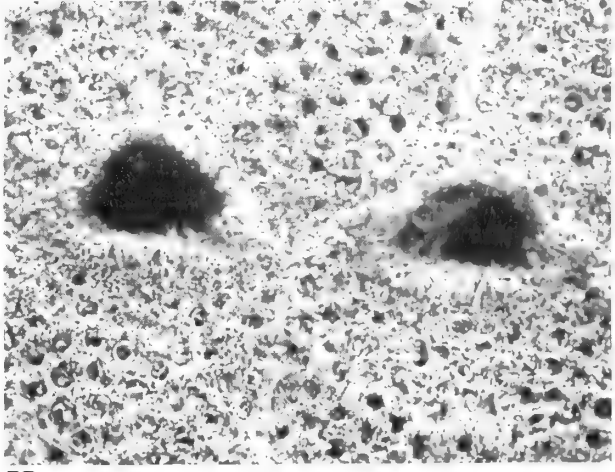
Figs 72–77 *Elea pseudolamellosa* sp. nov. 72–74, VH 10461, Upper Campanian, St Severin d'Uzel, Charente Maritime, France; 72, autozooids and eleozooids (top left), × 47; 73, autozooidal operculum, × 250; 74, autozooidal aperture, × 250. 75, VH 10462, holotype, Upper Campanian, St Severin d'Uzel, gonozooid origin with kenozooid above and to the left of the maternal zooid, × 65; 76, 77, VH 10471, Senonian, Le gare de Soullans, Vendée, France; 76, eleozooids and autozooids, × 65; 77, apertures of two eleozooids, × 250.
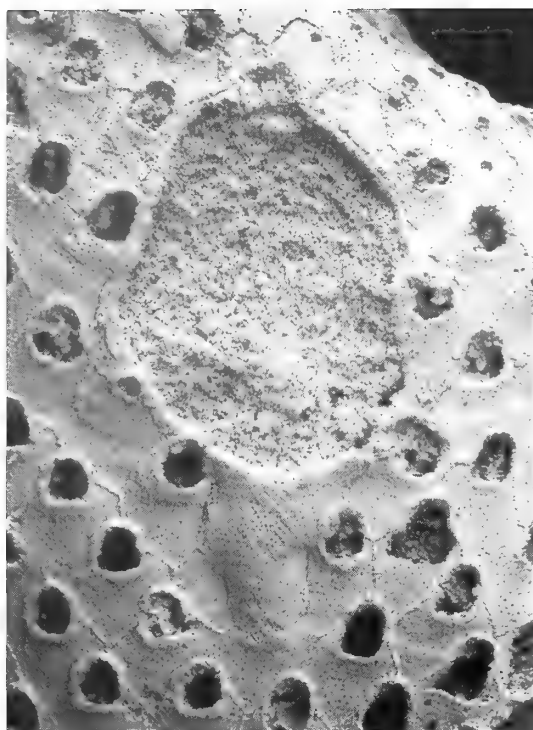
Fig. 78 *Elea pseudolamellosa* sp. nov., VH 10462, holotype, Upper Campanian, St Severin d'Uzel, Charente Maritime, France; gonozooid with broken roof, × 42.

Elea triangularis (Michelin, 1841)   Figs 87–94

1841   *Eschara triangularis* Michelin: 5, pl. 1, fig. 6.
1850   *Eschara triangularis* Michelin; d'Orbigny: 140.
1851   *Eschara triangularis* Michelin; d'Orbigny, pl. 602, figs 4 and 5.
1853   *Elea triangularis* (Michelin); d'Orbigny: 630, pl. 737, figs 17–20.
1890   *Elea triangularis* (Michelin); Pergens: 397.
1899   *Elea triangularis* (Michelin); Gregory: 305.
1975   *Elea triangularis* (Michelin); Walter: 314, pl. 29, figs 1, 5.

MATERIAL. Holotype: MNHN Michelin Collection un-numbered (Fig. 87), Albian, Grandpré, Ardennes, France. Other material: MNHN d'Orbigny Colln 6020 (5 pieces mounted on a tablet with the mark of a sixth, lost piece), same horizon and locality as holotype; BMNH 60541 (large colony and several fragments), 'Gault Chloritic' (probably Lower Albian *mammillatum* Zone according to H.G. Owen pers. comm.), Folkestone, Kent, UK; BMNH D52080 (SEM stub), Lower Albian (*tardefurcata* or *mammillatum* Zone, see Owen, 1972; Rawson *et al.*, 1978), Shenley Limestone, Leighton Buzzard, Bedfordshire, UK, R.J. Hogg Collection.

DESCRIPTION. Colony bifoliate (Fig. 87) with narrow, folded branches which bifurcate occasionally; branches generally 6
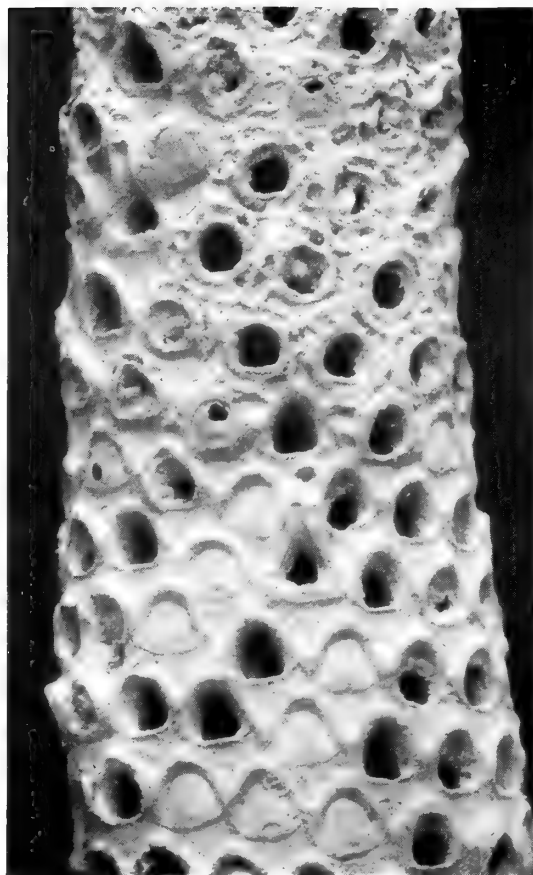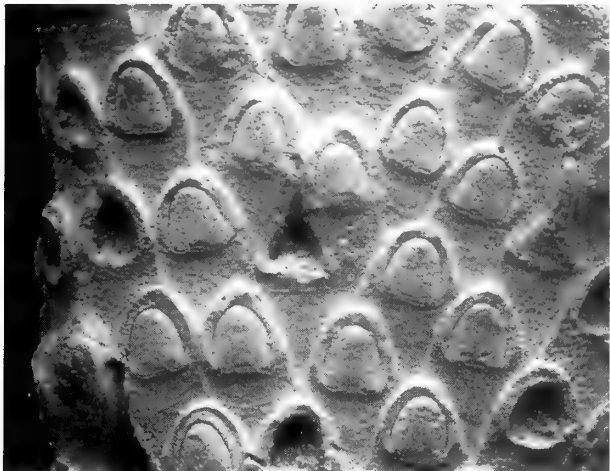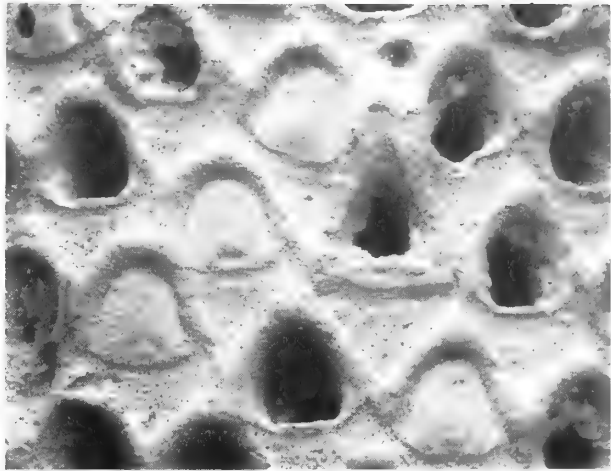

Fig. 79   *Elea subhexagona* sp. nov., ZMC Levinsen Collection M54, 'Turonien' [probably Cenomanian], St Calais, Sarthe, France; branch with autozooids, eleozooids and distally, an overgrowth of kenozooids occupying the areas between zooidal apertures; × 39.

mm wide and 1 mm deep. Zooids arranged in approximate quincunx; organization fixed-walled. Colony base hollow (in holotype). Growing edge often arcuate. Overgrowths sometimes developed on erect branches. Zooidal buds may be occluded by terminal diaphragms located well proximal to the interzooidal wall ends.

Autozooids (Fig. 89) medium-sized, generally rhombic with relatively short, convex frontal walls pierced by large, circular, slightly countersunk pseudopores; zooidal boundaries raised. Apertures (Fig. 90) very large, elongate, almost 1·5 × longer than wide, attaining maximum width a little distal to the hinge line, well-rounded distally; apertural shelf present only in the mid-part of the aperture, indenting the margins of the aperture and producing the bell-shape typical of the species; hinge line with a pair of prominent hinge teeth. Apertural rim thick, continuous with variably extensive but low tubercles at the lateral corners of the frontal wall. Opercula (Fig. 88) occasionally preserved in-situ, proximal edge a little concave, surface slightly convex, fissured and with about 25 elongate pseudopores arranged in an irregular crescent; internally (Fig. 92), prominent, inward-sloping sclerites form a continuous arch immediately outward of the pseudopores. Intramurally budded autozooids may be present. A tubular structure apparently composed of
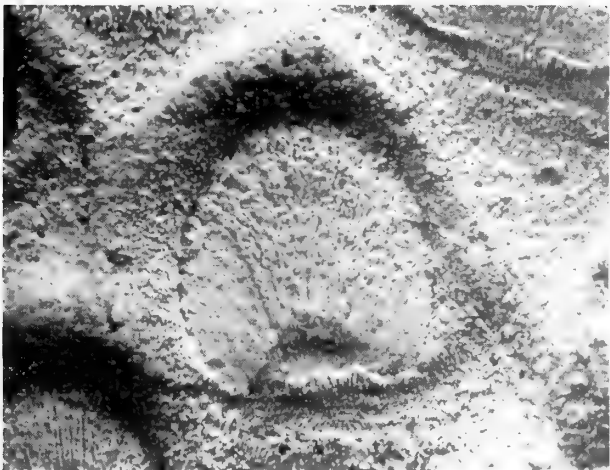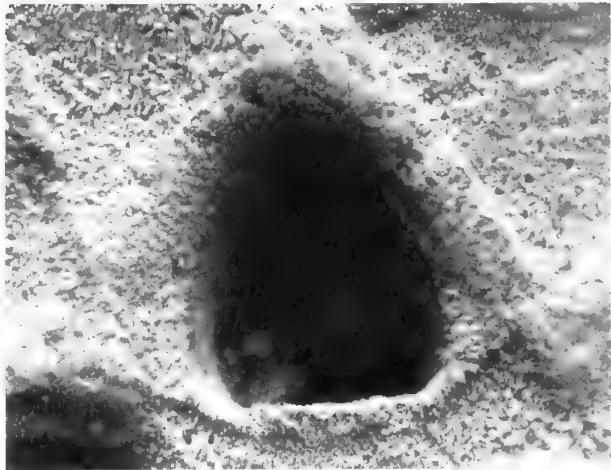
Figs 80–83 *Elea subhexagona* sp. nov. 80, DM un-numbered, Voigt photocard 2060, holotype, Upper Turonian, 'Oberen Pläners', Strehlen, Dresden, Germany, autozooids, mostly with opercula, and eleozooids, × 45. 81–83, ZMC Levinsen Collection M54, 'Turonien' [probably Cenomanian], St Calais, Sarthe, France; 81, autozooids and a primary eleozooid containing an intramural eleozooid, × 70; 82, autozooidal operculum, × 210; 83, autozooidal aperture, × 210.

pseudoporous exterior wall, which can be seen within the aperture of one zooid (Fig. 91), is interpreted as a bioclaustration (i.e. an embedment structure formed by the bryozoan; cf. similar structures in Cretaceous onychocellids attributed to the presence of folliculinid protists by Ernst, 1985). Interzooidal walls with conspicuous pores. Mural spines present in great abundance in the proximal parts of zooids, long, and either simple or branched (Fig. 93).

Eleozooids unknown, presumed absent.

Kenozooids sometimes present.

Gonozooid known from only one partly developed example (Fig. 94) showing the tubular, densely pseudoporous proximal part of the frontal wall emerging from the aperture of the maternal zooid.

MEASUREMENTS.

autozooids (10 zooids from BMNH 60531)

|	
frontal length:	mean = 0·55 mm; SD = 0·036 mm; CV = 6·6; range = 0·50–0·60 mm
frontal width: ·	mean = 0·35 mm; SD = 0·027 mm;
	CV = 7·8; range = 0·32–0·39 mm
apertural length:	mean = 0·29 mm; SD = 0·015 mm; CV = 5·2; range = 0·27–0·32 mm
apertural width:	mean = 0·20 mm; SD = 0·011 mm; CV = 5·2; range = 0·20–0·23 mm

REMARKS. The large size and characteristically bell-shaped autozooidal apertures immediately distinguish this uncommon species from others in the genus. *E. triangularis* is the only bifoliate melicerititid described from the Lower Cretaceous. It is also currently unique in being the only melicerititid known to possess mural spines (= zooecial or intrazooecial spines) (Fig. 93). Similar structures are, however, common and widely distributed taxonomically among non-melicerititid cyclostomes (see Farmer, 1979) and further investigations of the internal morphology of melicerititids will probably reveal more examples.

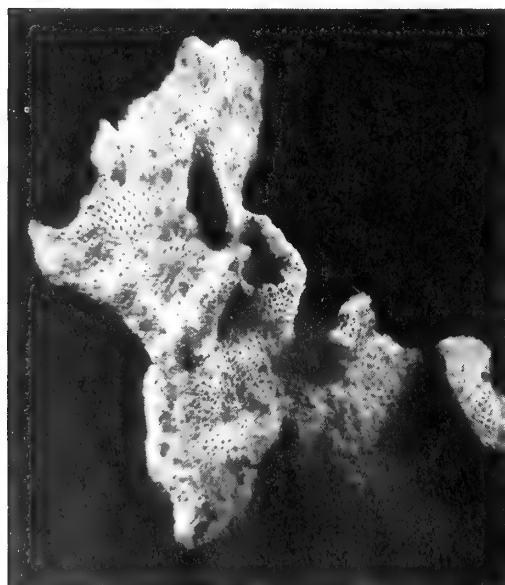DISTRIBUTION. Albian (?Lower Albian only) of France and England.
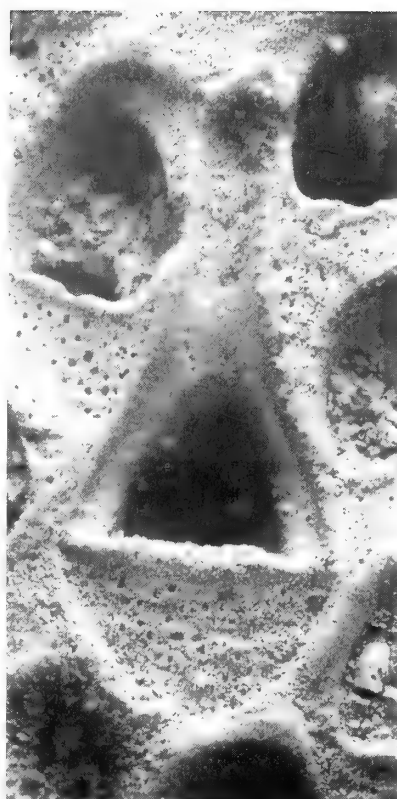
Figs 84–86 *Elea subhexagona* sp. nov. 84, DM un-numbered, Voigt photocard 2060, holotype, Upper Turonian, 'Oberen Pläners', Strehlen, Dresden, Germany, eleozooid with operculum, × 145. 85, 86, ZMC Levinsen Collection M53, 'Turonien' [probably Cenomanian], St Calais, Sarthe, France; 85, eleozooid, × 120; 86, damaged gonozooid, × 53.

Fig. 87 *Elea triangularis* (Michelin, 1841), photograph of the holotype colony, MNHN Michelin Collection un-numbered, Albian, Grandpré, Ardennes, France; × 2·5.

Fig. 88 *Elea triangularis* (Michelin, 1841), BMNH D52080, Lower Albian (*tardefurcata* or *mammillatum* Zone), Shenley Limestone, Leighton Buzzard, Bedfordshire, UK; secondary electron image of coated specimen showing autozooidal operculum in slightly oblique view, × 117.
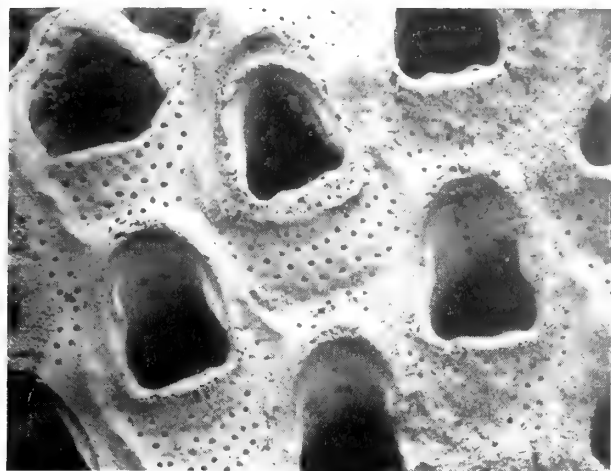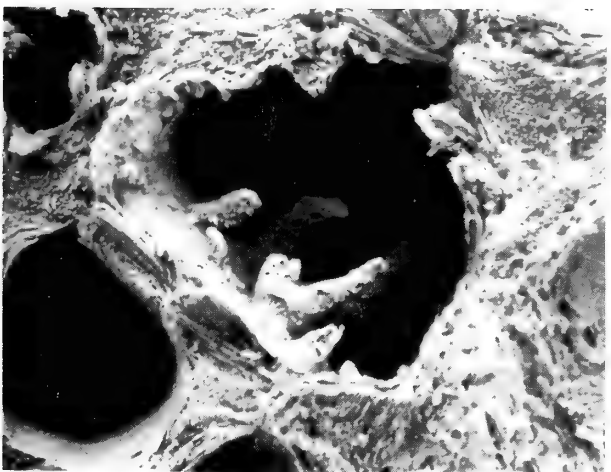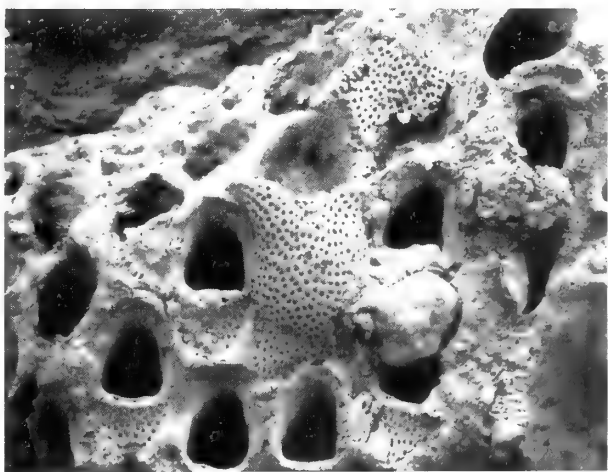
Figs 89–94 *Elea triangularis* (Michelin, 1841), BMNH 60531, 'Gault Chloritic' [probably Lower Albian *mammillatum* Zone], Folkestone, Kent, UK; 89, group of autozooids, including one with an intramural autozooid (upper centre), × 62; 90, autozooidal aperture, × 125; 91, autozooidal aperture containing enigmatic tubular structure, × 120; 92, inner side of an autozooidal frontal wall and operculum showing sclerites and pseudopores, × 118; 93, fractured specimen exposing mural spines within the proximal chamber of an autozooid, × 355; 94, proximal part of a broken gonozooid, × 37.

Elea viskovae sp. nov.   Figs 95–99

MATERIAL. Holotype: VH 10450, Turonian ('C22' division), Kyzylsaj, *ca* 180 km east of Fort Shevchenko, Kazakhstan, Najdin Collection. Paratypes VH 10542 (6 specimens), details as for holotype.

NAME. In honour of the Russian bryozoologist L.A. Viskova.

DESCRIPTION. Colony bifoliate with branches (Fig. 95) narrow, strap-like, bifurcating, about 1·3–2·0 mm wide and 0·5–0·6 mm deep. Autozooidal arrangement variable, both autozooids and eleozooids divergent close to branch margins; organization fixed-walled. Overgrowths common. Colony base unknown. One of the paratypes grows against and partially envelops a ?serpulid tube.

Autozooids (Fig. 96) large; frontal walls irregularly hexagonal, distally rounded, elongate, 2·5–3 × longer than wide, with circular pseudopores; zooecial boundaries raised. Apertures (Fig. 99) of moderate size, longitudinally elongate, on average 1·1 × longer than wide, attaining maximum width just proximal to mid-length, appreciably narrower at hinge line level, well-rounded distally; apertural shelf broad, 0·02–0·03 mm wide, causing the aperture to have the shape of a high isosceles triangle with rounded corners; apertural rim

Fig. 95 *Elea viskovae* sp. nov., VH 10450, holotype, Turonian ('C22' division), Kyzylsaj, *ca* 180 km east of Fort Shevchenko, Kazakhstan, Najdin Collection; branch with autozooids and marginal eleozooids, × 37.

moderately prominent; hinge line bowed. Opercula (Fig. 97) often preserved in-situ, slightly convex, with about 16 pseudopores arranged in a cresent parallel to the distal/lateral margin. Terminal diaphragms (Fig. 97) positioned proximally to the apertural shelf, ?non-pseudoporous. Intramural buds not observed with certainty.

Eleozooids (Figs 95, 96) common, located close to branch margins, about 2–2·5 longer than wide, their frontal walls a little longer and significantly wider than those of the autozooids. Aperture elongate, attaining maximum width slightly distally to the hinge-line, well-rounded distally; apertural shelf not clearly developed but rostral shelf present. Opercula known from only one partial example in-situ, surface strongly convex at preserved edges. Intramural buds not observed.

Kenozooids commonly present at branch margins.

Gonozooids not observed.

MEASUREMENTS.
autozooids (10 zooids with in-situ opercula from holotype VH 10450)

frontal length:	mean = 0·64 mm; SD = 0·070 mm; CV = 10·9; range = 0·54–0·77 mm
frontal width:	mean = 0·24 mm; SD = 0·024 mm; CV = 9·6; range = 0·21–0·29 mm
apertural length:	mean = 0·19 mm; SD = 0·009 mm; CV = 4·4; range = 0·18–0·21 mm
apertural width:	mean = 0·17 mm; SD = 0·010 mm; CV = 6·0; range = 0·17–0·20 mm

eleozooids (5 zooids from holotype VH 10450)

frontal length:	range = 0·63–0·80 mm
frontal width:	range = 0·32–0·35 mm
apertural length:	range = 0·27–0·30 mm
apertural width:	range = 0·21–0·24 mm

REMARKS. The marginal eleozooids of *Elea viskovae*, which resemble slightly-enlarged autozooids, distinguish this new species from others within the genus *Elea*. They have less well-developed rostra than those of *E. mackinneyi*, a species with smaller autozooids. Eleozooid morphology recalls that present in such species as *Meliceritites semiluna* and *Biforicula filicosa*.

Many of the autozooidal opercula (and some terminal diaphragms) in the holotype are pierced by small circular borings (Figs 96–97) like those described previously in other meliceritids (Taylor, 1982).

DISTRIBUTION. Turonian of Kazakhstan.

Elea whiteleyi sp. nov.   Figs 100–109

MATERIAL. Holotype: VH 10538, top Lower Cenomanian (*orbignyi* Zone) – basal Middle Cenomanian (*costatus* Zone), Saint-Germain-la-Campagne, descente sur Orbiquet, Eure, France, collected by G. Breton 1981. Paratypes: VH 10439, 10539–40, same horizon and locality as holotype. BMNH D55027–8, Cenomanian [?Lower Cenomanian, Craie Glauconieuse], Bruneval, Seine-Maritime, France, S. Whiteley Collection. Other material: VH, numerous un-numbered topotypes.

NAME. In honour of the late S. Whiteley, an enthusiastic amateur geologist who collected paratypes of this species.

DESCRIPTION. Colony bifoliate with bifurcating, narrow strap-like branches about 1·1–2·3 mm wide and 0·6 mm deep, elliptical in cross-section. Autozooids arranged more or less
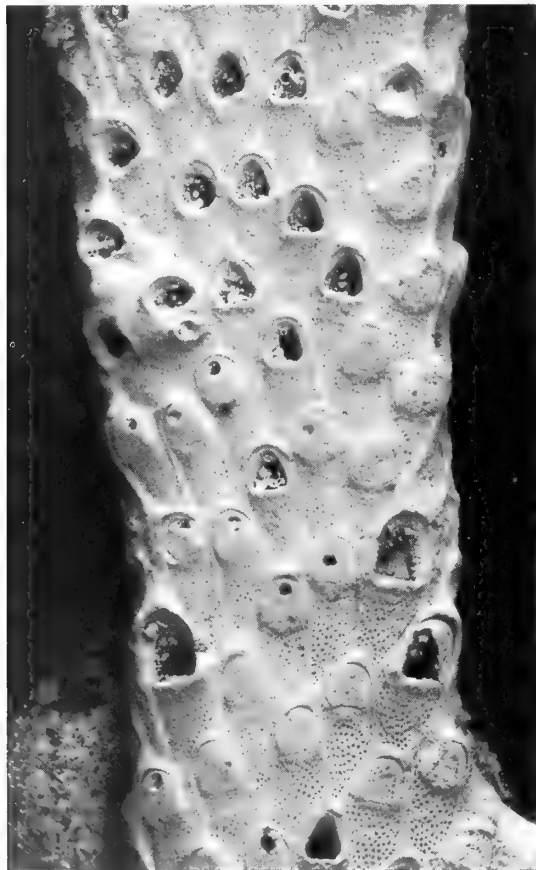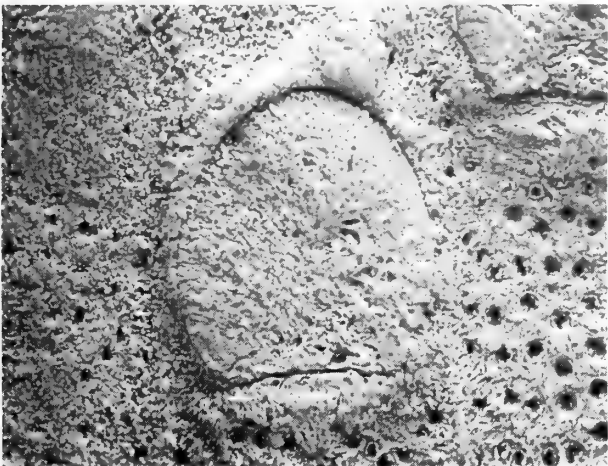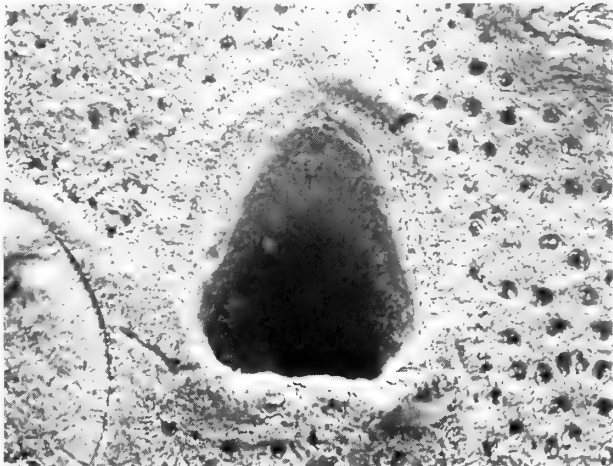
Figs 96–99 *Elea viskovae* sp. nov., VH 10450, holotype, Turonian ('C22' division), Kyzylsaj, *ca* 180 km east of Fort Shevchenko, Kazakhstan, Najdin Collection; 96, autozooids with opercula, some bored, and three marginal eleozooids, × 62; 97, bored autozooidal operculum (upper left) and terminal diaphragm (lower right), × 160; 98, autozooidal operculum, × 250; 99, autozooidal aperture, × 250.

in quincunx or in ill-defined transverse rows (Fig. 100), separated from adjacent autozooids by demizooids; organization fixed-walled. Overgrowths moderately common, at least some formed by eruptive budding onto surfaces of erect branches, sometimes consisting predominantly of demizooids and kenozooids . Colony base (Figs 105–107) extensive, giving rise to several erect branches whose median budding laminae are parallel to local orientation of basal zooids; demizooids of base have higher, more pointed apertures than those of erect branches, and many possess non-inclined apertures orientated parallel to adjacent autozooids.

Autozooids (Figs 102, 104) small, with longitudinally elliptical pseudoporous frontal walls, about twice as long as wide, depressed with respect to the surrounding demizooids. Apertures small, longitudinally elongate, about 1·1 × longer than wide, attaining maximum width at a level between the hinge line and mid-length; apertural shelf slight; apertural rim prominent, sometimes prolonged at the mid-point of the aperture; hinge line with a curved median bar. Opercula (Fig. 101) very often preserved in-situ, surface moderately convex, a flattened median proximal area often evident, bearing an estimated 14–18 slit-shaped pseudopores in a crescent close to the lateral/distal edge. Intramural buds and terminal diaphragms not observed.

Rostrozooids (Figs 105, 108) moderately common, usually occurring singly close to the branch mid-line just before a bifurcation, but sometimes located close to branch margins, elongate, about 3–5 × longer than wide. Aperture long, attaining maximum width at the hinge line, very slightly spatulate, rounded distally, about 3–4 × longer than wide. In-situ opercula not seen. Rostrozooids and/or demizooids may be budded intramurally within rostrozooids (Fig. 108).

Demizooids (Fig. 103) numerous, normally about 2 per autozooid, often paired disto-laterally on either side of an autozooidal aperture; frontal walls usually long and narrow, forming raised areas between frontal walls of laterally adjacent autozooids, their boundaries, however, poorly-defined; apertures variously orientated, many in oblique or reverse orientation with respect to colony growth direction, typically in a plane inclined about 60° to the colony surface, small, semicircular to longitudinally elongate in shape, rounded or slightly arched distally. Opercula often preserved in-situ; terminal diaphragms observed.
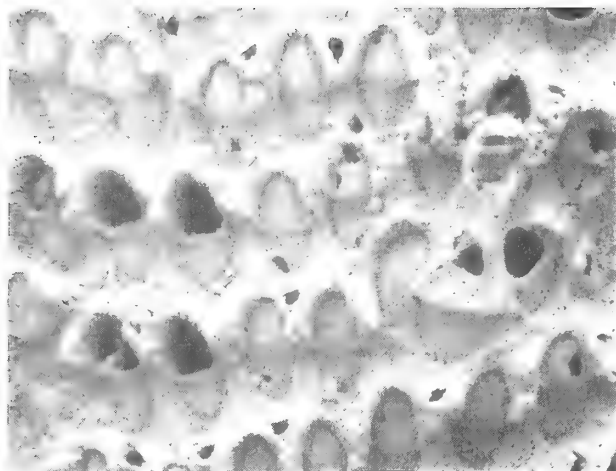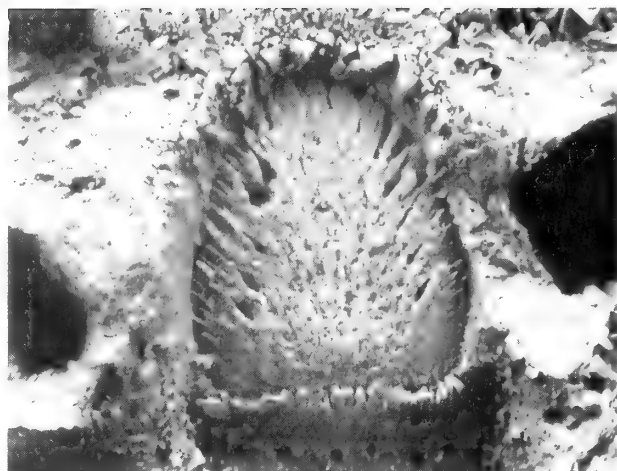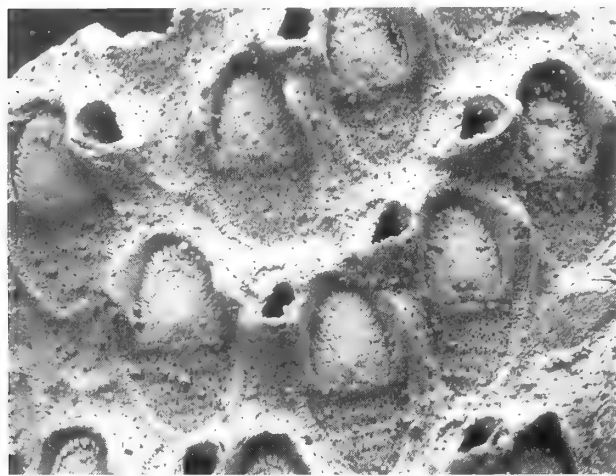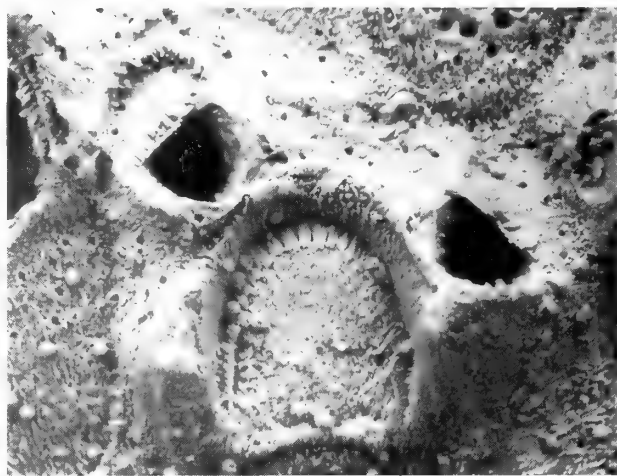
Figs 100–103 *Elea whiteleyi* sp. nov., top Lower Cenomanian (*orbignyi* Zone) – basal Middle Cenomanian (*costatus* Zone), Saint-Germain-la-Campagne, descente sur Orbiquet, Eure, France. 100–101, VH 10539; 100, branch surface, × 53; 101, autozooidal operculum, × 330. 102, 103, VH 10538, holotype; 102, autozooids, kenozooids, and demizooids with obliquely-directed, inclined apertures, × 95; 103, operculate autozooid and two demizooids, × 220.

Kenozooids (Figs 102, 105) observed commonly in colony base, overgrowths, and at the margins of erect branches.

Gonozooids (Fig. 109) fairly common. Distal frontal wall emerging from maternal aperture initially parallel-sided before becoming bulbous and longitudinally ovoidal in shape. Ooeciopore located beyond inflated part of frontal wall, transversely elliptical, about 1·5 × wider than long. Atrial ring not observed.

MEASUREMENTS.
autozooids (10 zooids with in-situ opercula from holotype VH 10538)

frontal length:	mean = 0·33 mm; SD = 0·015 mm; CV = 4·5; range = 0·30–0·35 mm
frontal width:	mean = 0·17 mm; SD = 0·008 mm; CV = 4·5; range = 0·17–0·18 mm
apertural length:	mean = 0·15 mm; SD = 0·005 mm; CV = 3·1; range = 0·15–0·17 mm
apertural width:	mean = 0·13 mm; SD = 0·006 mm; CV = 4·8; range = 0·12–0·14 mm

rostrozooids (5 zooids from 5 colonies)

frontal wall length:	range = 0·63–0·92 mm
frontal wall width:	range = 0·20–0·21 mm
apertural length:	range = 0·33–0·57 mm
apertural width:	range = 0·11–0·15 mm

demizooids

apertural width:	*ca* 0·06–0·09 mm

gonozooids (one zooid from holotype VH 10538)

total frontal wall length:	2·36 mm
dilated frontal wall length*:	1·13 mm
ooeciopore length:	0·08 mm
ooeciopore width:	0·12 mm

(* i.e. that part of the frontal wall distal to the narrow origin)

REMARKS. The presence of numerous small eleozooids enables this new species to be readily distinguished from all other species of *Elea*, including *E. elegantula* which it most
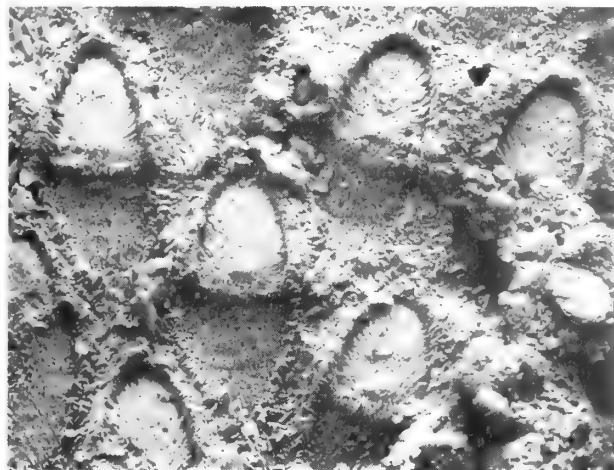
Figs 104–107 *Elea whiteleyi* sp. nov. 104, BMNH D55027 Cenomanian [?Lower Cenomanian, Craie Glauconieuse], Bruneval, Seine-Maritime, France, operculate autozooids (demizooids obscured by diagenetic cement), × 98. 105–107, VH 10439, top Lower Cenomanian (*orbignyi* Zone) – basal Middle Cenomanian (*costatus* Zone), Saint-Germain-la-Campagne, descente sur Orbiquet, Eure, France; encrusting colony base; 105, irregular arrangement of autozooids, kenozooids, small eleozooids and a large eleozooid, × 40; 106, large eleozooid (rostrozooid), × 100; 107, operculate autozooid and small eleozooid, × 135.

resembles in the morphology of the other polymorphs. These eleozooids and their distribution surrounding the autozooids invite comparison between *E. whiteleyi* and the Upper Cenomanian bifoliate melicerititid *Biforicula multicincta*, the oldest known species of *Biforicula* (see Voigt, 1989) The principal qualitative difference between *E. whiteleyi* and *B. multicincta* is the existence of cancelli in the latter. It therefore seems possible that *E. whiteleyi* belongs in the stem-group of *Biforicula*.

DISTRIBUTION. Lower-Middle Cenomanian of Normandy, France.

Genus *SEMIELEA* d'Orbigny, 1853

TYPE SPECIES. *Entalophora vieilbanci* d'Orbigny, 1850, designated by Bassler (1935: p. 198) as 'S. *vielbanci* D'Orbigny, 1853' [sic].

OTHER SPECIES. *Semielea dichotoma* d'Orbigny, 1853.

REVISED DIAGNOSIS. Eleid with tubular colony-form; axial lumen of subequal diameter lined by an inferred exterior wall; zooids in primary layer orientated parallel to tube length; autozooids fixed-walled; cancelli lacking.

REMARKS. D'Orbigny (1853) referred three species to *Semielea*. Only the first two are here retained in the genus; the third, *Semielea plana* d'Orbigny, 1853 is regarded as the base of *Elea lamellosa* (d'Orbigny, 1850) (see p. 19).

Diagnostic of *Semielea* is the possession of branches with an axial lumen, the bounding wall of which forms a lamina for zooidal budding. The axial lumen is intermediate in size between the narrow axial canals present in some species of *Meliceritites* (e.g. *M. semiclausa* (Michelin)) and the wide tubular interiors of certain specimens of *Reptomultelea* with cavariiform colonies. The growth of the axial lumen in *Semielea* also seems distinct. Although no specimens have

Fig. 108   *Elea whiteleyi* sp. nov., VH 10539, top Lower
Cenomanian (*orbignyi* Zone) – basal Middle Cenomanian
(*costatus* Zone), Saint-Germain-la-Campagne, descente sur
Orbiquet, Eure, France; primary rostrozooid containing
intramural rostrozooid in turn containing intramural
demizooid, × 120.

Fig. 109   *Elea whiteleyi* sp. nov., VH 10538, holotype, top Lower
Cenomanian (*orbignyi* Zone) – basal Middle Cenomanian
(*costatus* Zone), Saint-Germain-la-Campagne, descente sur
Orbiquet, Eure, France; gonozooid, × 50.

been studied with their microstructure sufficiently well-
preserved to prove that the wall which lines the lumen is an
exterior wall rather than an interior wall, the transverse
folding and wrinkling of this wall (Fig. 119) strongly suggests
that it is an exterior wall. Rare examples of colony bases
viewed from the underside (Fig. 122) show that the lumen of
each branch opens at the colony base and that the lumen wall
is smoothly continuous with the basal lamina. As the basal
lamina is an undoubted exterior wall, this observation is
further evidence that the lumen walls are exterior. In *S.
vieilbanci* occasional transverse platforms partition the axial
lumen and seem to have been formed by progressive constric-
tion of the lumen. The presence of these platforms, which
would have periodically sealed the entrance to the lumen at
branch growth tips, may explain why fouling of the apparent
exterior walls lining the lumen has not been observed (cf.
exterior walls lining the tubes of cavariiform *Reptomultelea*
colonies). The platforms also imply that branches could not
have grown around another erect organism (cf. some species
of *Reptomultelea*), but instead grew freely into space.

The phylogenetic relationship is unclear between *Semielea*
and species of *Meliceritites* on the one hand and of *Reptomul-
telea* on the other. Assuming *Semielea* to be a relatively
advanced genus, it could have derived from either of the two
latter genera. Derivation from *Meliceritites* would necessitate

the incorporation of tubular prolongations of the basal lamina
into the centre of the erect cylindrical branches, together with
loss of the normal endozonal budding pattern. Derivation
from *Reptomultelea* would require formation of tubular pro-
longations of the basal lamina to give erect cylindrical
branches. On the grounds of parsimony, the latter alternative
seems the more likely, but future phylogenetic analysis,
including zooid-level characters, might provide better evi-
dence of affinity.

DISTRIBUTION. Turonian (?Upper) – Lower Santonian,
northern France.

Semielea vieilbanci (d'Orbigny, 1850)   Figs 110–122

1850   *Entalophora vieilbanci* d'Orbigny: 200.
1851   *Diastopora vieilbanci* (d'Orbigny); d'Orbigny, pl. 637,
       figs 7–8.
1851   *Diastopora arborescens* d'Orbigny: pl. 638, figs 1–5.
1853   *Semielea vieilbanci* (d'Orbigny); d'Orbigny: 636, pl.
       738, figs 5–9.
1853   *Semimultelea arborescens* (d'Orbigny); d'Orbigny:
       652, pl. 741, fig. 5.
1890   *Semielea vieilbanci* (d'Orbigny); Pergens: 392.
1893   *Semielea vieilbanci* (d'Orbigny); Pergens: 211.
?1897a *Semielea vieilbanci* (d'Orbigny); Canu: 155.
?1897b *Semielea vieilbanci* (d'Orbigny); Canu: 750.
1899   *Elea vieilbanci* (d'Orbigny); Gregory: 300, fig. 33.

Fig. 110 *Semielea vielbanci* (d'Orbigny, 1850), photograph of MNHN d'Orbigny Collection 6965 (part), Turonian, France; × 8·5.

1912 *Meliceritites vielbanci* (d'Orbigny); Levinsen: 47, pl. 1, figs 15 and 16.
1953 *Semielea vielbanci* [sic] (d'Orbigny); Bassler: G77, fig. 40, 3a, b.
1981 *Semielea vielbanci* (d'Orbigny); Voigt: 453, fig. 5a.

MATERIAL. Type: there is no material of this species from the type locality (Turonian of Tourtenay; see d'Orbigny 1850, p. 200) in the d'Orbigny Collection, MNHN, although over a hundred specimens from the Turonian of several other localities are registered under number 6965 (e.g. Fig. 110). In view of the absence of topotype specimens, together with the unequivocal identity of the species, no neotype designation is made.

Other material: MNHN d'Orbigny Colln 6965, over 100 pieces from the Turonian of various localities in France, including Troot, St Maure, Tours, Angouleme, Villavard. MNHN d'Orbigny Colln 8200 (Figs 121, 122), Senonian, ?Villedieu, ?Vendôme, syntypes of *Diastopora arborescens* d'Orbigny, 1851, several specimens including Voigt Photocard 8312 and an un-numbered specimen corresponding to that illustrated by d'Orbigny (1851: pl. 638, fig. 2). ZMC Levinsen Colln unnumbered, Bruillé Poncé and Villedieu, France. VH unnumbered: U. Turonian, Souge; Turonian, Les Ulmes, Eure; U. Turonian, Bois de Gareau, nr Ecommoi, Sarthe; U. Turonian, Angoumien, La Charte sur la Loire; U. Turonian, Sougé, Loir-et-Cher; Turonian, Luynes, Indre et Loire; Turonian, Les Ulmes, Maine; U. Turonian, Troot, Loir-et-Cher; U. Turonian, Les Roches, Loir-et-Cher; Turonian, Les Ulmes, Maine; U. Turonian/Coniacian, La Barre, nr St Maure, Indre et Loire; Coniacian, St Paterne, Indre et Loire; Coniacian, Tours, Indre et Loire; Coniacian, Fécamp, Seine Maritime. BMNH D3747 (4), 'Senonian', Lavardin, Gamble Colln; D8959–60, 'Senonian', Lavardin; D4807, Craie de Villedieu [Coniacian or Santonian] , S. of les Roches; D467?, Craie de Villedieu, Luynes; D4679, D4800, D4806, D4860 (4), [Turonian], Montloire; D4675, D4676 (5), D4677, D4678 (4), D4683 (6), D4684 (3), D4715, D4799, D4811 (2), D4839, D4840 (3), D4861, D4862 (5), D4864 (2), D4865, D4868, D13573, Craie Marneuse, Villardin; D4937, [?Turonian], 'Nodula Chalk', Villardin Castle, purchd F.H. Butler; D4674 (figd Gregory, 1899: fig. 33), D4685, Craie Marneuse, Chinon; D33939–40, Turonian, St Calais, Sarthe, E. Darteville Colln; D36151–5, 'Senonian', Lavardin, Loir-et-Cher, Pergens Colln; D36156, Turonian, Lavardin, Loir-et-Cher, Pergens Colln; D53444, Turonian, Les Ulmes, Maine, Voigt Colln; D59368, Santonian, Craie de Villedieu, Bouchardière Mbr, Bed 20 of Jarvis *et al.* (1982), La Bouchardière, Villedieu, Loir-et-Cher; D59369 (3), Craie de Villedieu [Coniacian or Santonian], Luynes; D59370–2, D59373 (3), D59374 (6), D59375 (sample), Turonian, Lavardin, Loir-et-Cher, F. Canu Colln; D59376 (6), Turonian, Châtellerault, Vienne, France; BZ 729 (sample), Turonian, St Maure, Indre-et-Loire, France, presd E. Voigt, November 1991.

DESCRIPTION. Colony tubular (cavariiform) with branches (Fig. 110) bifurcating, normally subcircular in cross-section but becoming elliptical immediately prior to bifurcation, varying from about 1·0 to 4·4 mm in diameter, typically 3·5–4·5 mm. Axial lumen lined by transversely wrinkled, inferred exterior wall (Fig. 119) and generally 0·6–1·4 mm in minimum diameter, becoming elliptical in cross section prior to dividing at branch bifurcations. Single layer thickness about 0·3–0·5 mm. Budding apparently occurs only on the lumen-lining wall. Overgrowths occasionally present, originating through intrazooecial fission, either disc-shaped and multidirectional or fan-shaped and unidirectional (Fig. 118); pseudoancestrula an autozooid, aperture about 0·09 mm long by 0·08 mm wide, initiating a secondary zone of astogenetic change of increasing zooid size. Zooid apertures arranged in rough quincunx or in rows transverse to growth direction. Organization fixed-walled.

Autozooids (Figs 111, 115) of moderate size, frontally elongate, subhexagonal or subrhomboidal in outline, on average 1·7–1·8 × longer than wide, well-rounded distally; boundary wall salient, forming a widened wall with contiguous apertural rim at distal end of zooid; frontal wall flat proximally, sometimes slightly convex distally, pseudopores subcircular. Apertures (Fig. 113) small, occupying less than a third of the frontal area, approximately equidimensional or a little wider than long, attaining maximum width about midlength, well-rounded distally; apertural rim salient; apertural shelf of moderate width, tapering proximally; hinge line poorly preserved in all scanned specimens, bowed. Opercula (Fig. 112) often preserved in-situ, convex, prominent; pseudopores radially elongate, numbering about 16, arranged in a crescent. Terminal diaphragms (Fig. 117) common, located just proximally to the apertural shelf, with a central depression and pore. Intramurally budded autozooids not observed. Intramurally budded eleozooids (Fig. 111) very common; aperture (Fig. 114) trifoliate, prominent.
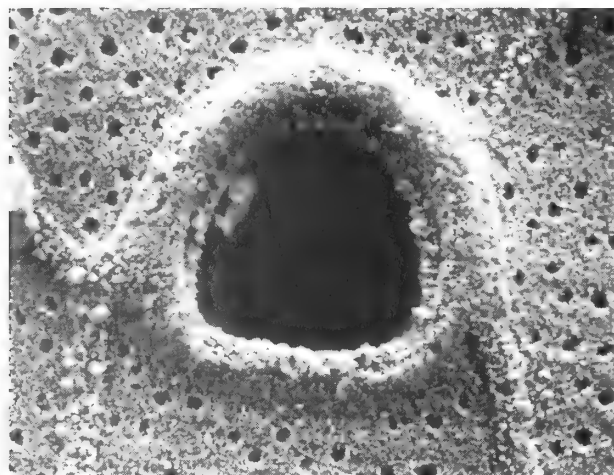
Kenozooids (Fig. 116) uncommon, developed close to branch bifurcations.
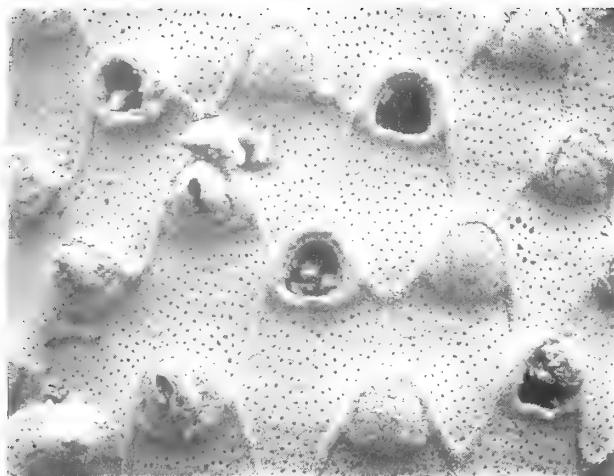
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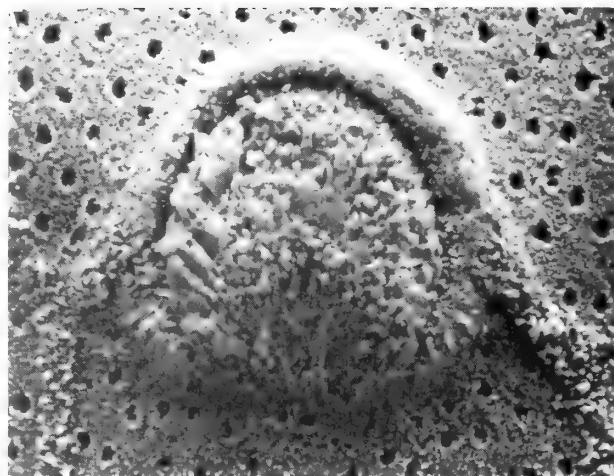
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Figs 111–114 *Semielea vieilbanci* (d'Orbigny, 1850), BMNH D59370, Turonian, Lavardin, Loir-et-Cher, France; 111, group of autozooids, some containing intramural eleozooids, × 75; 112, autozooidal operculum, × 330; 113, autozooidal aperture, × 330; 114, intramural eleozooidal aperture, × 365.

Eleozooids (Fig. 116) rare (excluding intramurally budded examples); frontally about the same length but narrower than the autozooids, pointed distally; aperture trifoliate; opercula not observed.

Gonozooids (Fig. 120) rare; frontally elongate, about twice as long as wide, the inflated frontal wall emerging from the maternal aperture initially parallel-sided, becoming longitudinally ovoidal distally. Ooeciopore and atrial ring not seen in poorly preserved specimens available for study.

MEASUREMENTS.

autozooids (10 zooids with in-situ opercula from BMNH D59370)

frontal length:	mean = 0·47 mm; SD = 0·030 mm; CV = 6·4; range = 0·42–0·53 mm
frontal width:	mean = 0·27 mm; SD = 0·019 mm; CV = 6·9; range = 0·26–0·30 mm
apertural length:	mean = 0·13 mm; SD = 0·007 mm; CV = 5·5; range = 0·12–0·14 mm
apertural width:	mean = 0·14 mm; SD = 0·009 mm; CV = 6·3; range = 0·12–0·15 mm

eleozooids (1 zooid from BMNH D36151)

frontal length:	0·48 mm
frontal width:	0·20 mm
apertural length:	0·09 mm
apertural width:	0·04 mm

gonozooids (2 zooids from BMNH D4674)

total frontal length:	1·86–1·91 mm
dilated frontal wall length:	1·56–1·65 mm
frontal width:	0·90–0·98 mm

REMARKS. This is a very common species. Most specimens come from the Upper Turonian of the Loire region of France, but the species ranges upwards into the Coniacian and evidently even into the basal Santonian. The wide axial lumen immediately distinguishes *S. vieilbanci* from similarly dendroid species of *Meliceritites* which, at most, only have narrow axial canals a little wider than the zooecial chambers. The small size of the apertures, particularly in comparison with frontal wall dimensions, distinguishes *S. vieilbanci* from
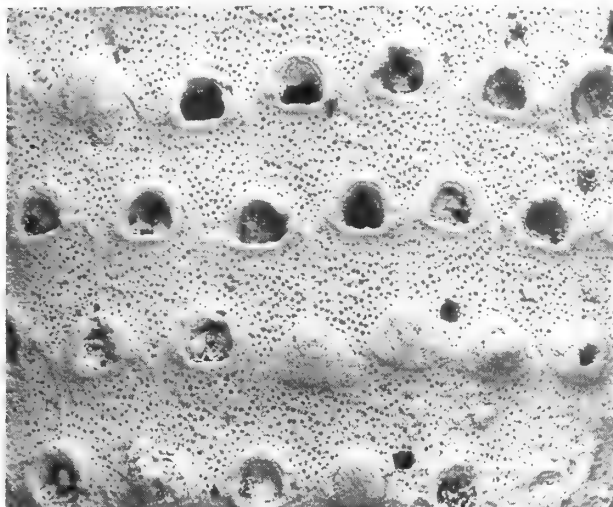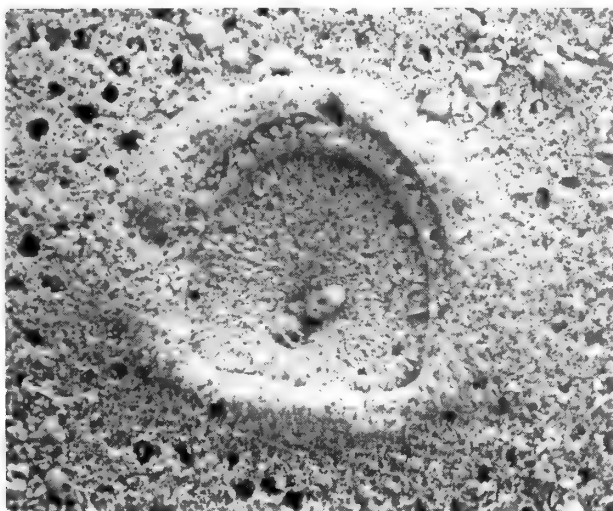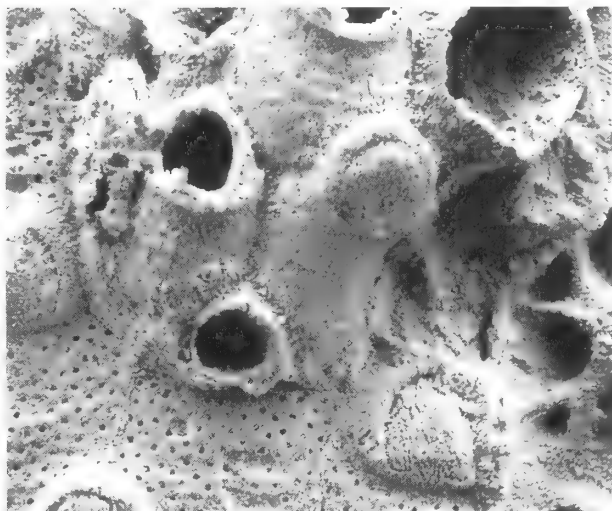
Figs 115–118   *Semielea vieilbanci* (d'Orbigny, 1850). 115–117, BMNH D36151, 'Senonian', Lavardin, Loir-et-Cher, France; 115, autozooids arranged in transverse rows, × 60; 116, autozooids, kenozooids and an eleozooid (centre) close to a branch bifurcation, × 100; 117, autozooidal aperture with terminal diaphragm, × 340. 118, BMNH D59371, Turonian, Lavardin, overgrowth origin, × 135.

S. dichotoma, and both species of *Semielea* differ from cavariiform colonies of *Reptomultelea* spp. in the consistently parallel orientation of the long axes of the zooids and the tubular branches.

DISTRIBUTION. Turonian (?Upper) – Lower Santonian, northern France.

### *Semielea dichotoma* (d'Orbigny, 1851)   Figs 123, 124

1851   *Diastopora dichotoma* d'Orbigny: pl. 638, figs 6–8.
1853   *Semielea dichotoma* (d'Orbigny); d'Orbigny: 637.
1890   *Semielea dichotoma* (d'Orbigny); Pergens: 393.
1912   *Meliceritites dichotoma* (?) (d'Orbigny); Levinsen: 38, pl. 5, figs 1 and 2.

MATERIAL. Lectotype: MNHN d'Orbigny Collection 8194 (Figs 123–124), specimen labelled as 'type' by E. Voigt, Voigt Photocard No. 8321, Senonian [?Coniacian], Tours, Indre et

Loire, France. This specimen, a fragment 21 mm long which resembles but does not exactly match plate 638, figure 6 of d'Orbigny (1851), is one of several specimens of various species contained in six tubes and registered as 8194. No other material is available for study. E. Voigt (in litt. April 1984) states that 'Although I have got much material from Tours, I have never found this species in the French Turonian'.

DESCRIPTION. Colony tubular (cavariiform) with bifurcating branches (Fig. 123) about 2–3 mm in diameter. Overgrowths not observed. Organization fixed-walled. Zooid apertures variously arranged, often irregular.

Autozooids (Fig. 124) with short frontal walls. Apertures large, frontally elongate or equidimensional, closely-spaced, well-rounded distally; apertural rims thick and protruberant, especially distally; apertural shelf broad. Opercula often preserved in-situ, strongly convex and prominent. Terminal
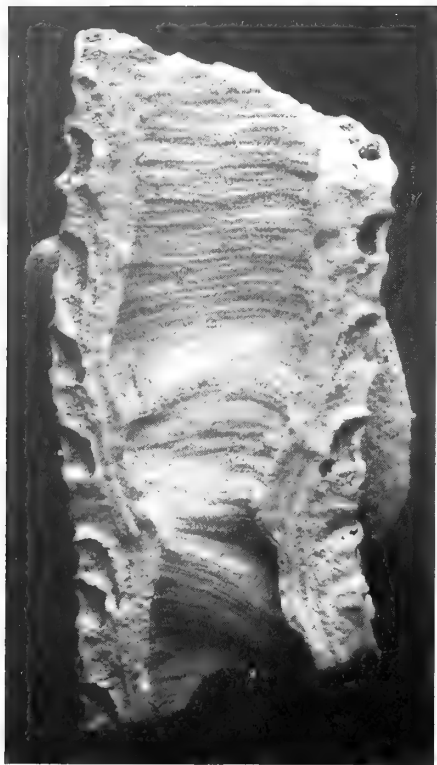
Fig. 119 *Semielea vieilbanci* (d'Orbigny, 1850), BMNH D59372, Turonian, Lavardin, Loir-et-Cher, France; longitudinally fractured branch showing axial lumen with wrinkled lining wall, × 21.

diaphragms with a transverse depression present in many zooids. Intramurally budded eleozooids present; aperture triangular in shape, longer than wide.

Kenozooids not observed.

Eleozooids (except intramural buds) of uncertain presence. Gonozooids not observed.

MEASUREMENTS (approximate determinations taken from the lectotype MNHN d'Orbigny Collection 8194, Voigt Photocard 8321).

autozooids
apertural length: *ca* 0·21–0·25 mm
apertural width: *ca* 0·20–0·22 mm

eleozooids (probably intramurally budded)
apertural length: *ca* 0·17 mm
apertural width: *ca* 0·13 mm

REMARKS. The description given above is based on examination of the lectotype using an optical microscope during a visit to the MNHN in 1985. Unfortunately, the species has not been studied using SEM and therefore detailed morphological information is lacking (type specimens from the d'Orbigny Collection, regrettably and much to the detriment of scientific knowledge, are not available for loan).

Semielea dichotoma differs from *S. vieilbanci* in having larger and more prominent autozooidal apertures which occupy a high proportion of the zooidal frontal surface, and intramurally budded eleozooids with triangular apertures.

Fig. 120 *Semielea vieilbanci* (d'Orbigny, 1850), BMNH D4674, Craie Marneuse, Chinon, France; gonozooid with broken frontal wall and sediment-obscured ooeciopore, × 53.

DISTRIBUTION. Senonian (?Turonian) of the Loire Region, France.

Genus *REPTOMULTELEA* d'Orbigny, 1853

TYPE SPECIES. *Reptomultelea tuberosa* d'Orbigny, 1853: p. 655, by monotypy, subjective junior synonym of *Reptelea sarthacensis* d'Orbigny, 1853: p. 640.

OTHER SPECIES. *Reptomultelea acclivata* sp. nov., *R. auris* sp. nov., *R. betusora* nom. nov. (for *Diastopora tuberosa* Reuss, 1874), *R. bituberosa* sp. nov., *Semimultelea canui* Voigt, 1924, *R. convexa* sp. nov., *S. dixoni* Lang, 1906, *Meliceritites filiozati* Levinsen, 1912, *R. goldfussi* sp. nov., *R. levinseni* sp. nov., *R. matutina* sp. nov., *R. mitrus* sp. nov., *Diastopora oceani* d'Orbigny, 1850, *R. parvula* sp. nov., *R. pegma* sp. nov., *Semimultelea polytaxis* Voigt, 1924, *R. pseudopalpebrosa* sp. nov., *R. reedi* sp. nov., *Semielea reussi* Pergens, 1890, *R. sarissata* Gregory, 1899, *R. scanica* sp. nov., *Clausimultelea tuberculata* d'Orbigny, 1853.

REVISED DIAGNOSIS. Eleid with encrusting, unilamellar or multilamellar colony; autozooids fixed-walled; cancelli lacking.

REMARKS. *Reptomultelea* is employed for a broad grouping of 23 fixed-walled meliceritids with non-erect, unilamellar
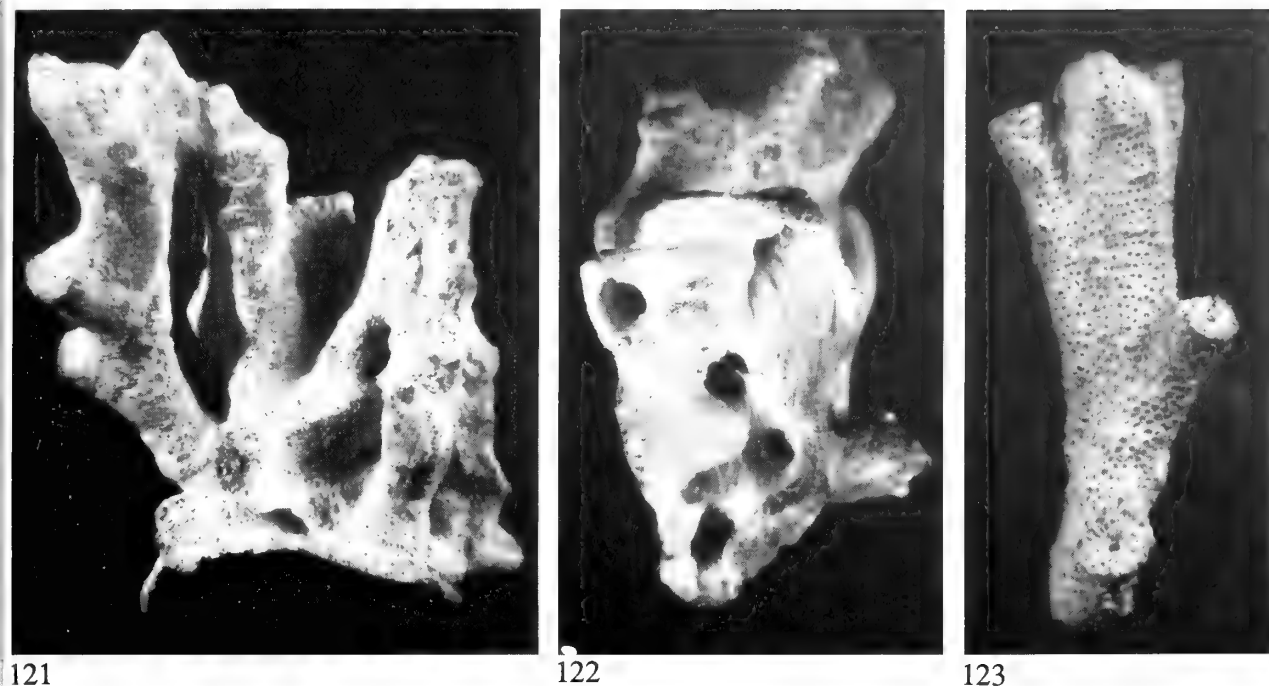
121   122   123

Figs 121–123 *Semielea* spp., photographs. 121–122, *S. vielbanci* (d'Orbigny, 1850), MNHN d'Orbigny Collection 8200, Senonian, ?Villedieu, ?Vendôme, syntype of *Diastopora arborescens* d'Orbigny, 1851; 121, profile of colony with intact base; 3·2; 122, underside of base showing entrances to the axial lumens of four branches, × 4·1. 123, *S. dichotoma* (d'Orbigny, 1853), MNHN d'Orbigny Collection 8194, lectotype, Senonian [?Coniacian], Tours, Indre et Loire, France, × 3·7.

Fig. 124 *Semielea dichotoma* (d'Orbigny, 1853), photograph of MNHN d'Orbigny Collection 8194, lectotype, Senonian [?Coniacian], Tours, Indre et Loire, France; autozooids (some with opercula) and eleozooids (?intramural), × 38.

or, more often, multilamellar colonies. The oldest known species is *R. matutina* sp. nov. from the Lower Albian Shenley Limestone of Bedfordshire, England, and the youngest is *R. scanica* sp. nov. from the Lower Campanian of Scania, Sweden. Considerably more species (12) are recorded

from the Cenomanian than from any other stage (see Fig. 127).

Table 4 is a key to species identification and should be used in conjunction with Figures 125 and 126 which depict the outline shapes of autozooidal and eleozooidal apertures. The species of *Reptomultelea* are fairly easy to separate if the material available is sufficient to access the character states of the autozooids and eleozooids. Variation between the small number of specimens available is relatively large for three of the new species (*R. convexa*, *R. goldfussi* and *R. mitrus*) recognized here. It is possible that one or more of these species will eventually require taxonomic splitting when further specimens become available.

Species of *Reptomultelea* are generally easily distinguished from the encrusting bases of erect melicerititids because of their large areal extent, typically multilamellar growth, regularity and generally high proportion of autozooids relative to eleozooids and kenozooids. Among species founded for non-erect colonies of melicerititids, *Reptoceritites rowei* Gregory, 1899 and *Reptoceritites acutissima* Voigt, 1963 fail to meet these criteria and are considered to be the encrusting bases of colonies of *Meliceritites* rather than species of *Reptomultelea*.

A difficult problem concerns the phylogenetic relationships between species of *Reptomultelea* and species of erect fixed-walled melicerititids belonging particularly to *Meliceritites* and *Elea*. Zooid-level characteristics, including eleozooid morphology, can be more similar between given species of *Reptomultelea* and erect species of these genera than with other species of *Reptomultelea*. For example, the intramural eleozooids of *R. pseudopalpebrosa* sp. nov. greatly resemble those of *Meliceritites palpebrosa* Levinsen, while the pointed eleozooids of *R. tuberculata* recall similar structures in *M.*
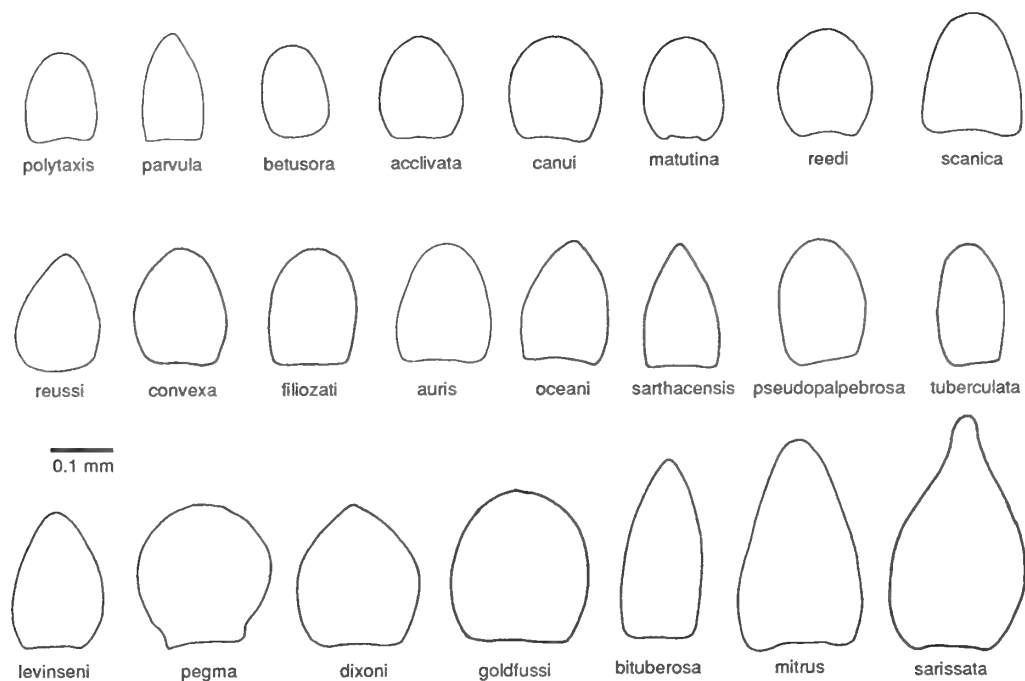
Fig. 125 Outlines of autozooidal aperture shapes in species of *Reptomultelea*. Individual apertures were traced from SEM micrographs and scaled using the mean apertural length determined for the species. Species are arranged according to apertural length.

Fig. 126 Outlines of eleozooidal aperture shapes in species of *Reptomultelea*. Individual apertures were traced from SEM micrographs and scaled using the mean apertural length determined for the species. Species are arranged according to apertural length.
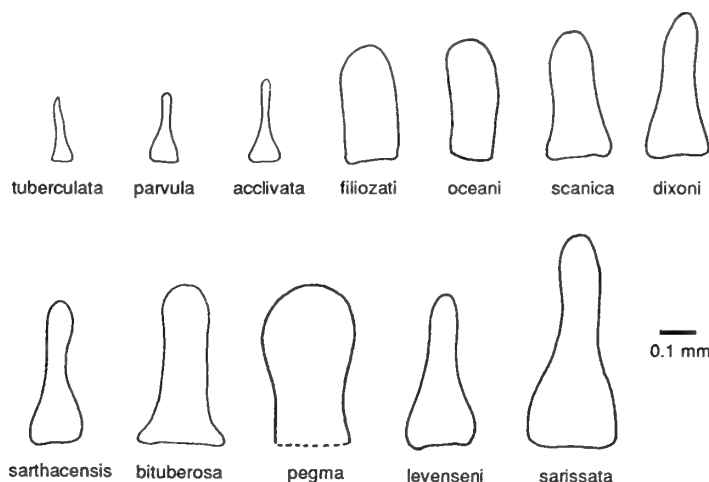
gothica Levinsen and several related species of *Meliceritites*. Such similarities raise the possibility that *Reptomultelea* is not monophyletic but may instead be polyphyletic or paraphyletic. The polyphyletic hypothesis necessitates convergent evolution of species of *Reptomultelea* from various erect meliceritid species by parallel loss of the erect branches of colonies, together with enlargement of the encrusting colony base, seemingly a relatively simple evolutionary option. The paraphyletic hypothesis necessitates convergent evolution of species of erect meliceritids from the primitive 'genus' *Reptomultelea*. This is a less attractive alternative because (1)

it demands the acquisition of erect growth several times, and (2) stratigraphical evidence suggests that *Reptomultelea* is not the most primitive meliceritid genus because the early Albian appearance of *Reptomultelea* post-dates the late Barremian appearance of *Meliceritites* by a significant time period. However, a full phylogenetic analysis of the meliceritids is needed to decide whether *Reptomultelea* is monophyletic, polyphyletic or paraphyletic. Until this has been accomplished, monophyly is assumed if only for reasons of nomenclatoral stability and pragmatic taxonomy.

Other genera established for encrusting meliceritids

Table 4 Key to the species of *Reptomultelea*. Note, because this key places a high reliance on eleozooids, which may not be developed in every specimen, identifications should be carefully checked against the full descriptions. Furthermore, it is possible that new material will reveal the presence of eleozooids in species in which they are currently unknown.

1. Eleozooids present 2
   Eleozooids absent 20
2. Eleozooid apertures larger than autozooids (i.e. rostrozooids) 3
   Eleozooid apertures smaller than autozooids 14
3. Autozooid apertures very wide, more than 0·20 mm 4
   Autozooid apertures narrower, less than 0·20 mm 5
4. Autozooid apertures ogee arch-shaped, more than 0·35 mm long .... *R. sarissata* (p.94)
   Autozooid apertures very slightly pointed, less than 0·30 mm long .... *R. dixoni* (p.69)
5. Eleozooid rostrum broad, well-rounded distally 6
   Eleozooid rostrum narrow, pointed or poorly-rounded distally 10
6. Opercula deeply depressed distally; apertural shelf very wide; eleozooid rostrum spatulate .... *R. pegma* (p.85)
   Otherwise 7
7. Zooids with a pair of prominent tubercles at either end of the hinge line .... *R. bituberosa* (p.63)
   Otherwise 8
8. Autozooid frontal wall short (less than 0·50 mm); aperture occupying a high proportion of the frontal area .... *R. scanica* (p.95)
   Otherwise 9
9. Eleozooid frontal wall longer than 0·85 mm .... *R. oceani* (p.80)
   Eleozooid frontal wall shorter than 0·85 mm .... *R. filiozati* (p.71)
10. Autozooid apertures very tall (length about 1·5 × width); eleozooid apertures only slightly longer than autozooid apertures; kenozooids numerous .... *R. tuberculata* (p.97)
    Otherwise 11
11. Eleozooid rostrum well-raised distally so that plane of aperture is oblique to colony surface .... *R. acclivata* (p.54)
    Otherwise 12
12. Zooids very small – e.g. autozooid frontal wall width less than 0·21 mm; eleozooid frontal wall length less than 0·50 mm .... *R. parvula* (p.82)
    Otherwise 13
13. Zooids medium-sized – e.g. autozooid frontal wall length less than 0·59 mm; eleozooid frontal wall length less than 0·90 mm .... *R. sarthacensis* (p.49)
    Zooids larger .... *R. levinseni* (p.74)
14. Eleozooid apertures inverted T-shaped (trifoliozooids) 15
    Otherwise 18
15. Autozooids commonly with small kenozooids forming 'ears' on either side of the aperture .... *R. auris* (p.57)
    Otherwise 16
16. Autozooid frontal wall less than 0·45 mm long .... *R. polytaxis* (p.85)
    Otherwise 17
17. Autozooid aperture less than 0·15 mm wide .... *R. betusora* (p.59)
    Autozooid aperture more than 0·15 mm wide ...... *R. convexa* (p.66)
18. Eleozooid apertures D-shaped with a hood-like area distally .... *R. pseudopalpebrosa* (p.89)
    Eleozooid apertures tall and pointed 19
19. Autozooid apertures less than 0·20 mm wide . *R. canui* (p.65)
    Autozooid apertures more than 0·20 mm wide .... *R. reussi* (p.91)
20. Autozooid apertures less than 0·15 mm wide ...... *R. matutina* (p.77)
    Otherwise 21
21. Autozooid apertures lancet arch-shaped ...... *R. mitrus* (p.79)
    Autozooid apertures rounded 22
22. Autozooid apertures less than 0·21 mm long; crescentic arrangement of opercular pseudopores .... *R. reedi* (p.91)
    Autozooid apertures more than 0·21 mm long; pseudopores scattered widely over operculum .... *R. goldfussi* (p.73)

include *Reptelea* d'Orbigny, 1853, *Semimultelea* d'Orbigny, 1853, *Clausimultelea* d'Orbigny, 1853 and *Reptoceritites* Gregory, 1899. Lang (1906), who revised the 'reptant eleids', used *Reptelea* for unilamellar species lacking eleozooids ('avicularia'), *Reptoceritites* for unilamellar species with eleozooids, *Semimultelea* for bilamellar/multilamellar species lacking eleozooids, and *Reptomultelea* for bilamellar/multilamellar species with eleozooids (*Clausimultelea* he regarded as belonging to the non-melicerititid family Clausidae). The type species of *Reptelea*, *Reptelea pulchella* d'Orbigny, 1853, is of uncertain identity but may be the base of a colony of *Elea lamellosa* (d'Orbigny, 1850) (see p. 19), that of *Semimultelea*, *S. irregularis* d'Orbigny, 1853 is also the base of an *Elea lamellosa* colony (see p. 19), while that of *Reptoceritites*, *R. rowei* Gregory, 1899, is the base of a colony of *Meliceritites dollfusi* Pergens, 1890. Therefore, *Reptelea*, *Semimultelea* and *Reptoceritites* have no value as genera for the reception of non-erect melicerititid species as they all represent basal parts of erect taxa. Lang's (1906) scheme for the generic division of melicerititids must be rejected. *Clausimultelea*, type species *C. tuberculata* d'Orbigny (see p. 99), is merely a *Reptomultelea* with an above average proportion of kenozooids.

Semielea d'Orbigny, 1853, type species *S. vieilbanci* d'Orbigny, 1853 (see p. 43), is retained as a genus distinct from *Reptomultelea* despite the fact that cavariiform colonies of various species of *Reptomultelea* (e.g. *R. auris*, *R. convexa*, *R. reussi*) may closely resemble *Semielea*. These species of *Reptomultelea* show variable orientations of zooids in the initial layer whereas the zooids are orientated strictly parallel to the branch axis in *Semielea*. Furthermore, it is probable that cavariiform colonies of *Reptomultelea* grew loosely around erect organisms like hydroids (cf. many modern cavariiform cheilostomes). In contrast, the existence of 'platforms' partitioning the axial tubes shows that this was not the case in colonies of *Semielea*.

DISTRIBUTION. Lower Albian – Lower Campanian (Fig. 127), Europe and western Asia.

Reptomultelea sarthacensis d'Orbigny, 1853   Figs 2, 128–147

1826   *Cellepora escharoides* Goldfuss: 28 (partim), pl.12, figs 3b–c only.
1853   *Reptelea sarthacensis* d'Orbigny: 640, pl. 604, figs 9–10, pl. 738, fig. 15.
1853   *Reptomultelea tuberosa* d'Orbigny: 655, pl. 741, figs 14–15.
1872   *Diastopora oceani* d'Orbigny; Reuss: 110 (partim), pl. 27, fig. 2 only.
1877   *Diastopora acupunctata* Novák: 99 (partim), pl. 6, fig. 1 only.
1890   *Semielea sarthacensis* (d'Orbigny); Pergens: 393.
1897a *Semielea sarthacensis* (d'Orbigny); Canu: 155, pl. 5, fig. 10.
1897b *Semielea sarthacensis* (d'Orbigny); Canu: 749.
non 1899   *Reptomultelea tuberosa* d'Orbigny; Gregory: 320, fig. 37 [=*Reptomultelea bituberosa* sp. nov., see p. 63].
1912   *Melicerititites sarthacensis* (d'Orbigny); Levinsen: 41, pl. 1, figs 1–2.
?1938 *Reptoceritites zahálkai* Prantl: 31, pl. 2, fig. 9.

MATERIAL. Holotype: MNHN d'Orbigny Collection 6562

(Fig. 129), Cenomanian, Le Mans, Sarthe, France; this colony encrusts a concavity in a sponge.

Other material: MNHN d'Orbigny Colln 6589 (Fig. 128), Cenomanian, Le Mans; presumed to be the holotype of *R. tuberosa*. PSUB Goldfuss Colln 105B, Cenomanian, Essen, Germany; presumed to be the specimen figured by Goldfuss (1826: pl. 12, figs 3b, c) as *Cellepora escharoides*. SMD un-numbered, specimen figured by Reuss (1872: pl. 27, fig. 2) as *Diastopora oceani* d'Orbigny (Voigt photocard 2814), Cenomanian, *plenus* Zone, Dresden-Plauen, Germany. EM RE 551.763.31.A711, Cenomanian, Essen. VH 10432, 10472, Lower Cenomanian, Mülheim-Broich, Westfalia, Germany. VH 10437–8, top of Lower Cenomanian (*orbignyi* Zone) or base of Middle Cenomanian (*costatus* Zone), Saint-Germain-la-Campagne, Calvados, France, Breton Colln. VH 10463, Lower Turonian, St Calais, Sarthe, France. VH 10466, Upper Cenomanian, St Calais. VH 10510, Upper Cenomanian (*plenus* Zone), Dresden-Plauen, Germany. BMNH D3624 (2 specimens), D3631, Cenomanian, Essener Grünsand, Essen, Westfalia, Germany. BMNH D4424 [only the specimen on a serpulid tube], Cenomanian [*plenus* Zone], Korycaner Schichten, Kamajk, Bohemia, Czechoslovakia. BMNH D54294, Upper Cenomanian or Lower Turonian, nr St Calais, Sarthe, France, Voigt Colln. BMNH D54304–5, Upper Cenomanian (*plenus* Zone), Predboj, Bohemia, Czechoslovakia, Voigt Colln. BMNH D58952–8, Upper Cenomanian (*gourdoni* Zone), Craie glauconieuse à *Metiococeras* et *Sciponoceras*, St Calais road-cutting, Sarthe, Taylor & Hammond Colln.

Questionably assigned: BMNH D59244–6, Chloritic Marl, [Lower Cenomanian], St Catherine's Point, Isle of Wight, England.

DESCRIPTION. Colony unilamellar or multilamellar (Fig. 2), individual layers about 0·21–0·27 mm thick and occasionally growing free of the substratum with a transversely folded basal lamina. Ancestrula not identified unequivocally; autozooids from primary zone of astogenetic change with smaller, more rounded apertures than those from zones of repetition. Overgrowths (Figs 131, 141) originate by intrazooecial fission of one or more basal zooids; pseudoancestrula an autozooid, often surrounded by 6 daughter zooids, sometimes depressed
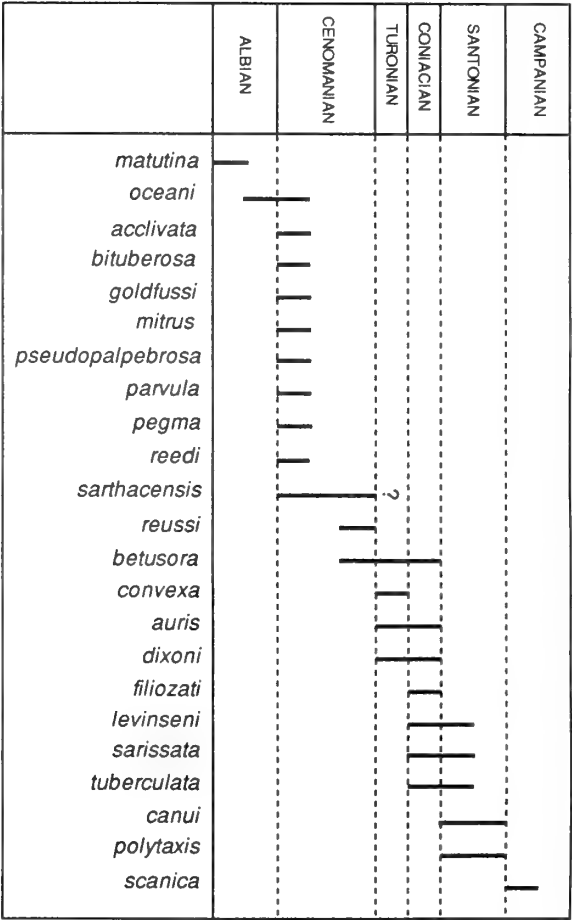
	ALBIAN	CENOMANIAN	TURONIAN	CONIACIAN	SANTONIAN	CAMPANIAN
matutina	■					
oceani	■					
acclivata		■				
bituberosa		■				
goldfussi		■				
mitrus		■				
pseudopalpebrosa		■				
parvula		■				
pegma		■				
reedi		■				
sarthacensis		■——?——	■			
reussi		■				
betusora			■———	■		
convexa			■			
auris			■———	■		
dixoni			■———	■		
filiozati				■		
levinseni				■———	■	
sarissata				■———	■	
tuberculata				■———	■	
canui					■	
polytaxis					■	
scanica						■

Fig. 127 Stratigraphical ranges of species of *Reptomultelea*.

beneath general level of colony surface but occasionally raised (possibly as a result of intramural budding); autozooids in secondary zone of astogenetic change with smaller and more rounded apertures than those in zone of repetition.

128

129

Figs 128, 129 *Reptomultelea sarthacensis* (d'Orbigny, 1853), photographs. 128, MNHN d'Orbigny Collection 6589, Cenomanian, Le Mans, France; presumed to be the holotype of *R. tuberosa* d'Orbigny, 1853; × 3·6. 129, MNHN d'Orbigny Collection 6562, Cenomanian, Le Mans, France; holotype of *Reptelea sarthacensis* d'Orbigny, 1853, showing autozooids, eleozooids and a gonozooid, × 18.

Organization fixed-walled. Zooids variably arranged, often approximately quincuncial.

Autozooids (Fig. 130) moderately small, frontally elongate, about 1·6–2 × longer than wide, often hexagonal in outline, occasionally diamond-shaped, with a pointed distal end; frontal wall occupying about half of the frontal surface, slightly convex, with circular pseudopores; boundary wall well-defined, salient. Aperture (Figs 132, 139) of medium size, on average about 1·5 × longer than wide, gothic arch-shaped, pointed distally, attaining maximum width somewhere between the hinge line and mid-length; apertural rim well-developed, raised to form a tubercle-like protuberance at the pointed distal end of the aperture; apertural shelf narrow; hinge line with low teeth at either end of a median bar. Operculum (Figs 133, 140) often preserved in-situ, convex, with about 24 radially ovoidal pseudopores arranged in a crescent close to the disto-lateral edge. Terminal diaphragms rarely present, located beneath level of apertural shelf, some with scattered pseudopores and a central depression. Intramural buds not observed.

Eleozooids (Figs 142–145) abundant, scattered; moderately large, frontal surface generally about 2·5 × longer than wide, considerably longer and usually a little wider than the autozooids; frontal wall occupying about half or less of the frontal surface, convex with pseudopores as in the autozooids. Aperture elongate, generally 2–3 × longer than wide, attaining maximum width at or a little distally of the hinge line, with a long, narrow rostral area sometimes a little spatulate; rostrum generally depressed at its distal end; hinge line with a wide median bar with small teeth at either end. Opercula rarely preserved in-situ. Terminal diaphragms (Fig. 142) may be present. Intramurally budded eleozooids (Fig. 145) and ?autozooids present.

Kenozooids variable in abundance, scattered or aggregated, often present immediately distal to eleozooids (Fig. 143) or in areas of disrupted growth (Figs 137, 146).

Gonozooids (Figs 146–147) moderately common, longitudinally elongate, 1·5–2 × longer than wide, a short parallel-sided portion emerging from the maternal aperture and becoming ovoidal to pear-shaped. Ooeciopore (Fig. 138) transversely elongate, variable in width, its distal edge indented internally by a hemiseptum. Atrial ring not observed.

MEASUREMENTS.
autozooids
(10 zooids from BMNH D54294)

frontal length:	mean = 0·48 mm; SD = 0·026 mm; CV = 5·5; range = 0·44–0·51 mm
frontal width:	mean = 0·26 mm; SD = 0·019 mm; CV = 7·2; range = 0·23–0·29 mm
apertural length:	mean = 0·21 mm; SD = 0·017 mm; Q: CV = 8·0; range = 0·18–0·24 mm
apertural width:	mean = 0·14 mm; SD = 0·012 mm; Q: CV = 8·6; range = 0·12–0·15 mm

(10 zooids from EM RE 551.763.31.A711)

frontal length:	mean = 0·51 mm; SD = 0·035 mm; CV = 6·9; range = 0·48–0·59 mm
frontal width:	mean = 0·25 mm; SD = 0·018 mm; CV = 7·1; range = 0·23–0·27 mm
apertural length:	mean = 0·18 mm; SD = 0·022 mm; CV = 12·1; range = 0·15–0·23 mm
apertural width:	mean = 0·13 mm; SD = 0·016 mm;

CV = 12·8; range = 0·11–0·17 mm

(10 zooids from VH 10432)

frontal length:	mean = 0·55 mm; SD = 0·030 mm; CV = 5·5; range = 0·51–0·59 mm
frontal width:	mean = 0·27 mm; SD = 0·024 mm; CV = 8·8; range = 0·24–0·32 mm
apertural length:	mean = 0·23 mm; SD = 0·017 mm; CV = 7·3; range = 0·21–0·26 mm
apertural width:	mean = 0·15 mm; SD = 0·009 mm, CV = 5·7; range = 0·14–0·17 mm

eleozooids
(8 zooids from BMNH D54294)

frontal length:	mean = 0·74 mm; SD = 0·054 mm; CV = 7·3; range = 0·68–0·83 mm
frontal width:	mean = 0·29 mm; SD = 0·023 mm; CV = 7·7; range = 0·26–0·33 mm
apertural length:	mean = 0·49 mm; SD = 0·041 mm; CV = 8·4; range = 0·44–0·54 mm
apertural width:	mean = 0·19 mm; SD = 0·013 mm; CV = 6·5; range = 0·17–0·21 mm

(7 zooids from EM RE 551.763.31.A711)

frontal length:	mean = 0·81 mm; SD = 0·029 mm; CV = 3·6; range = 0·78–0·86 mm
frontal width:	mean = 0·31 mm; SD = 0·036 mm; CV = 11·5; range = 0·27–0·38 mm
apertural length:	mean = 0·50 mm; SD = 0·050 mm; CV = 10·1; range = 0·44–0·59 mm
apertural width:	mean = 0·17 mm; SD = 0·029 mm; CV = 16·4; range = 0·15–0·23 mm

(8 zooids from VH 10432)

frontal length:	mean = 0·70 mm; SD = 0·037 mm; CV = 5·3; range = 0·63–0·75 mm
frontal width:	mean = 0·27 mm; SD = 0·017 mm; CV = 6·6; range = 0·24–0·30 mm
apertural length:	mean = 0·38 mm; SD = 0·019 mm; CV = 5·1; range = 0·36–0·41 mm
apertural width:	mean = 0·16 mm; SD = 0·011 mm; CV = 7·0; range = 0·15–0·18 mm

gonozooids
(1 zooid from holotype MNHN d'Orbigny Collection 6562)

frontal length:	*ca* 1·43 mm
dilated frontal length:	*ca* 1·30 mm
frontal width:	*ca* 0·81 mm
ooeciopore length:	*ca* 0·09 mm
ooeciopore width:	*ca* 0·10 mm

(2 zooids from VH 10432)

|	
frontal length:	1·58–1·74 mm
dilated frontal length:	1·37–1·53 mm
frontal width:	0·75–0·90 mm
ooeciopore length:	0·08 mm
ooeciopore width:	0·14–0·18 mm

REMARKS. Pergens (1890) first recognized that *Reptomultelea tuberosa* d'Orbigny, 1853 was a junior synonym of *R. sarthacensis*, the latter species having been described in the same publication but with page priority. *R. tuberosa* is the type species, by monotypy, of *Reptomultelea* d'Orbigny, 1853, and therefore *R. sarthacensis* is considered to be the correct name for the type species of this genus. Gregory's (1899) *R. tuberosa* d'Orbigny is a different species, redescribed as *R. bituberosa* sp. nov. (p. 63).
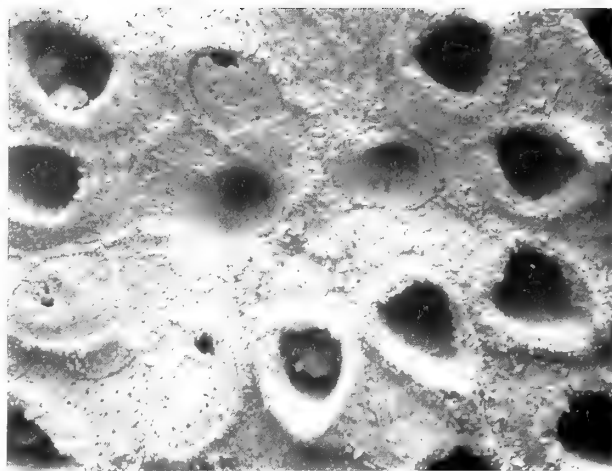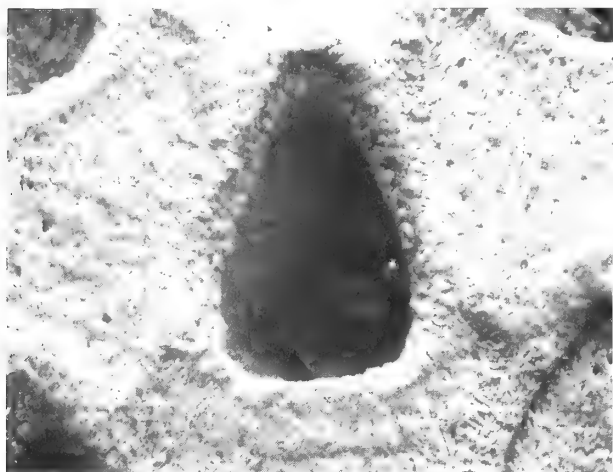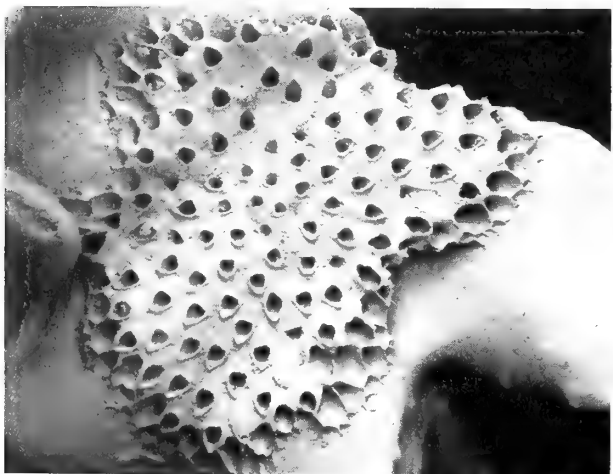
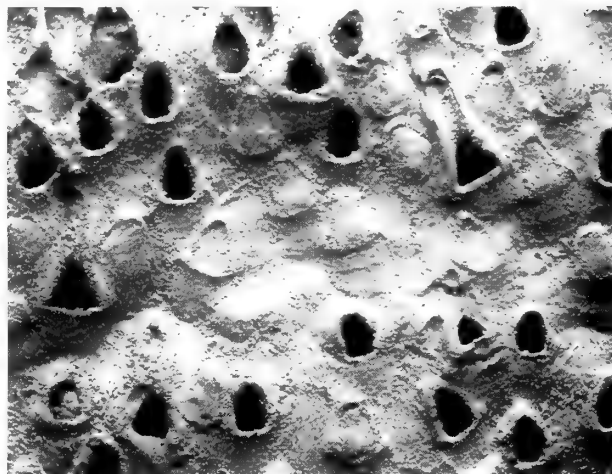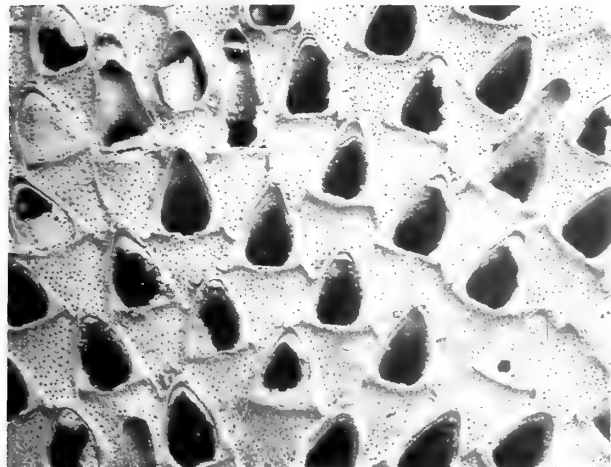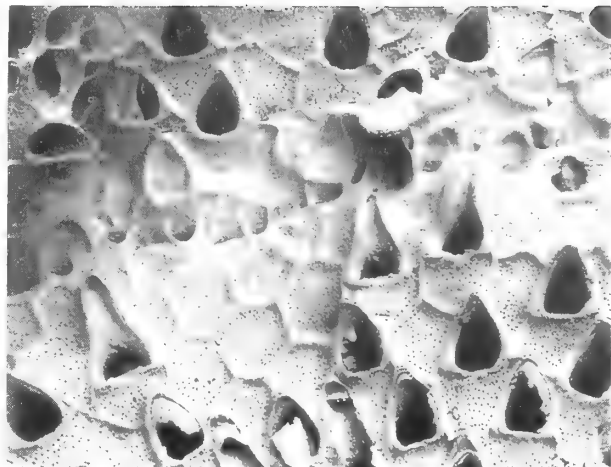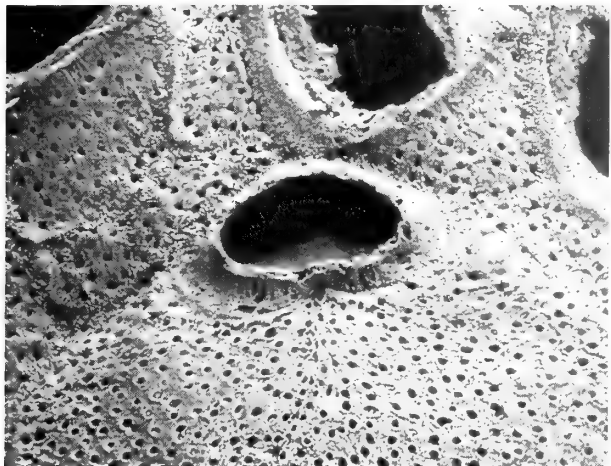**Figs 130–135** *Reptomultelea sarthacensis* (d'Orbigny, 1853). 130–133, BMNH D54294, Upper Cenomanian or Lower Turonian, nr St Calais, Sarthe, France; 130, autozooids and an eleozooid, × 72; 131, two depressed pseudoancestrulae surrounded by radiating autozooids, × 105; 132, autozooidal aperture, × 230; 133, autozooidal operculum, × 225. 134, VH 10463, Lower Turonian, St Calais, Sarthe, France; small colony encrusting a shell, × 15. 135, EM RE 551.763.31.A711, Cenomanian, Essen, Germany; depressed area of colony showing autozooids (with and without opercula) and eleozooids, × 35.
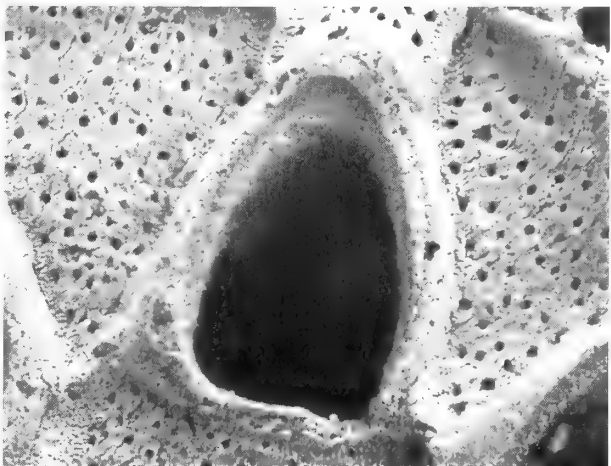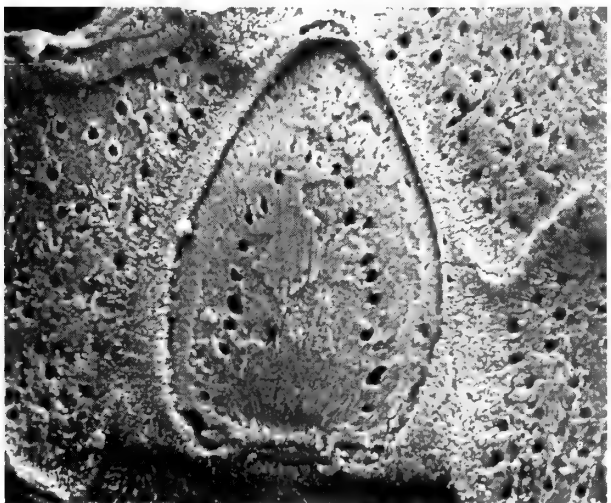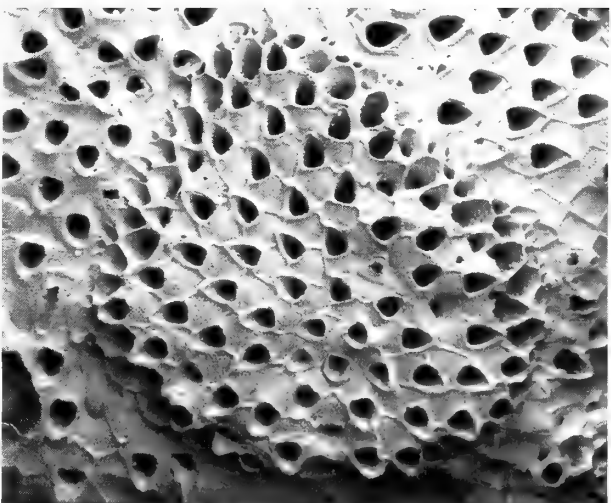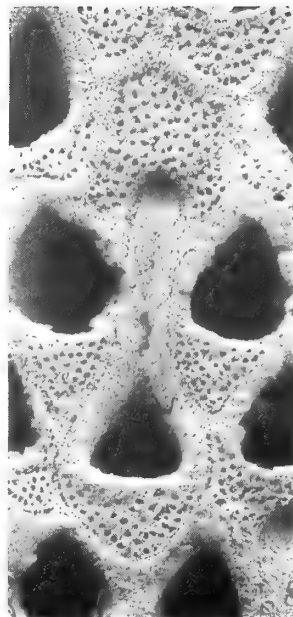
Figs 136–141 *Reptomultelea sarthacensis* (d'Orbigny, 1853), VH 10432 Lower Cenomanian, Mülheim-Broich, Westfalia, Germany; 136, autozooids (some with broken opercula) and eleozooids, × 48; 137, edge of overgrowth showing disrupted area with kenozooids and eleozooids, × 40; 138, ooeciopore, × 137; 139, autozooidal aperture, × 200; 140, autozooidal operculum, × 250; 141, newly-developed overgrowth, × 21.

142   143   144   145

Figs 142–145 *Reptomultelea sarthacensis* (d'Orbigny, 1853), variation in eleozooidal morphology. 142, VH 10432 Lower Cenomanian, Mülheim-Broich, Westfalia, Germany; eleozooid with broad, almost parallel-sided rostrum and the remains of a terminal diaphragm, × 100. 143, VH 10510, Upper Cenomanian (*plenus* Zone), Dresden-Plauen, Germany; eleozooid with narrow, slightly spatulate rostrum resting on a distal kenozooid, × 75. 144, BMNH D54294, Upper Cenomanian or Lower Turonian, nr St Calais, Sarthe, France; eleozooid with narrow, slightly spatulate rostrum, × 120. 145, EM RE 551.763.31.A711, Cenomanian, Essen, Germany; eleozooid with broad, slightly spatulate rostrum and hosting an intramural eleozooid, × 92.

The type specimen of *Reptoceritites zahálkai* Prantl, 1938, from the Turonian of Bohemia, was not available for study during a visit in June 1986 to the Narodni Museum, Prague, and Prantl's illustration of a worn specimen is inadequate for positive identification of the species. However, topotype specimens (BMNH D54304–5) collected by Professor E. Voigt are conspecific with *R. sarthacensis*.

One of the two specimens (SMD un-numbered; Voigt photocard 2814) from the *plenus* Zone of Dresden figured by Reuss (1872) as *Diastopora oceani* d'Orbigny appears to be a unilamellar colony of *R. sarthacensis* encrusting an oyster (pl. 27, fig. 2). Pergens (1890: p. 399) recognized that the *D. oceani* of Reuss was not the same as d'Orbigny's species and proposed *Semielea reussi* for *D. oceani* sensu Reuss. *S. reussi* is not placed in synonymy with *R. sarthacensis* because the second of Reuss's syntype specimens (pl. 27, fig. 3) is a different species and is here selected as the lectotype of *S. reussi* (see p. 91).

Among the material described from the Czechoslovakian Cenomanian/Turonian as *Diastopora acupunctata* Novák, 1877, is at least one specimen belonging to *R. sarthacensis*. This is the specimen shown in plate 6, fig. 1 of Novák (1877) and registered in the Narodni Museum as 2437 (Voigt photocards 6455 and 6458).

As here delimited, *R. sarthacensis* is a widely distributed species ranging from the Lower Cenomanian to the Upper Cenomanian or possibly Lower Turonian. Some morphometric differences exist between populations, but the unity of the species is supported by the ubiquitous long, narrow eleozooid rostra and gothic arch-shaped autozooid apertures with dis-

tally raised rims. Colonies from the Lower Cenomanian of Westfalia tend to have eleozooid rostra rather broader than those of younger populations, and an above average proportion of kenozooids occurs in specimens from the Essener Grünsand. The short but variable length of the eleozooid rostra in material from the Lower Cenomanian of the Isle of Wight (BMNH D59244–6) could be due to environmental stunting or might indicate a specific distinction; therefore, these specimens are questionably assigned to *R. sarthacensis*.

Reptomultelea levinseni sp. nov. (p. 74) from the Coniacian/Santonian of northern France is very similar to *R. sarthacensis* but has appreciably longer autozooid and eleozooid frontal walls.

DISTRIBUTION. Lower Cenomanian-Upper Cenomanian or Lower Turonian. Known from the Lower Cenomanian of Germany, ?France and ?England; ?Middle Cenomanian of France; Upper Cenomanian of Germany, France and Czechoslovakia.

Reptomultelea acclivata sp. nov.   Figs 148–154

MATERIAL. Holotype: VH 10427, Lower Cenomanian, Mülheim-Broich, Westfalia, Germany. Paratype: VH 10502, same horizon and locality as holotype. Other material: VH un-numbered, several topotype colonies.

NAME. Acclivata, Latin for upward slope, with reference to the upward-sloping eleozooid rostra.

DESCRIPTION. Colony unilamellar or multilamellar, each
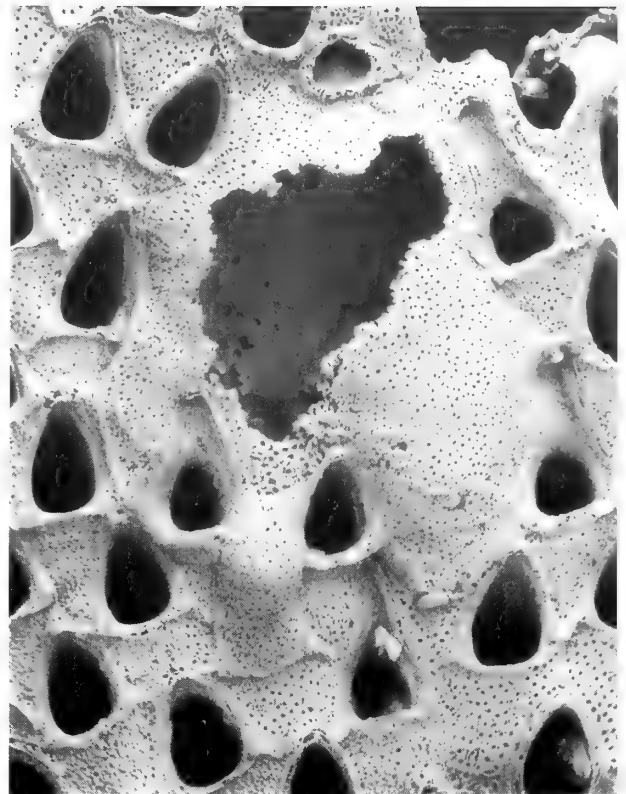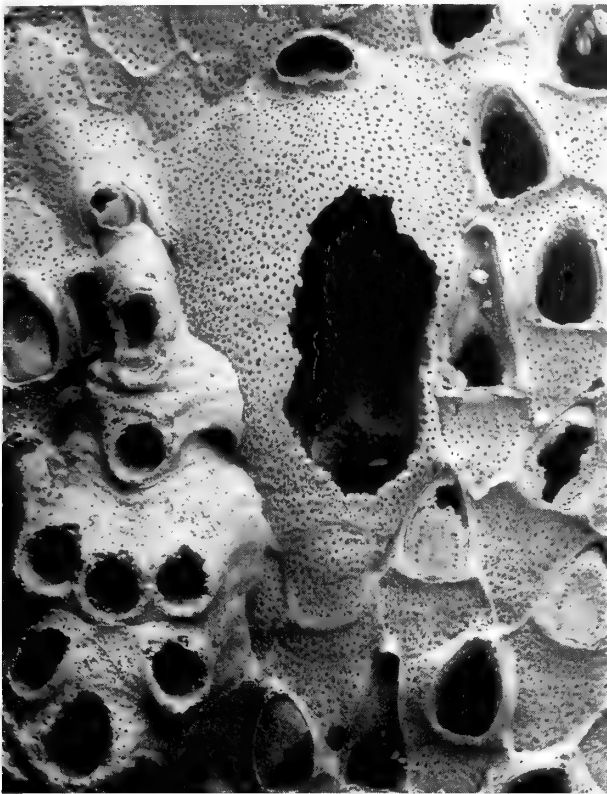
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Figs 146, 147 *Reptomultelea sarthacensis* (d'Orbigny, 1853), gonozooids, VH 10432 Lower Cenomanian, Mülheim-Broich, Westfalia, Germany; 146, gonozooid with broken frontal wall; note fouling tubuliporine cyclostome which has become enveloped proximally by an overgrowth of melicerititid kenozooids, × 60; 147, two coalescent gonozooids sharing a single ooeciopore, × 70.

layer about 0·23 mm thick, often growing free of the substratum and with a transversely folded basal lamina. Ancestrula not observed. Overgrowths (Figs 148–149) presumed to originate by intrazooecial fission; pseudoancestrulae with depressed apertures, small (*ca* 0·08–0·09 mm), more or less equidimensional and less pointed than apertures of autozooids from zone of astogenetic repetition. Organization fixed-walled. Zooids arranged in irregular quincunx.

Autozooids (Figs 150, 152) small, frontally elongate, about twice as long as wide, subhexagonal with a moderately pointed distal end; frontal wall generally occupying more than half of frontal surface, pseudopores subcircular; boundary wall poorly defined, subdued. Aperture of small size, slightly elongate, about 1·1–1·2 × longer than wide, widest between the hinge line and mid-length, slightly arched to rounded distally; apertural rim well-developed distally where it may be prolonged into a pointed projection; hinge line bowed, detailed structure unclear; apertural shelf very narrow or absent. Operculum (Fig. 151) sometimes preserved in-situ, flat centrally but with slightly convex sides, possessing about 20 slit-like pseudopores arranged in a crescent parallel to the disto-lateral edge; inner surface with narrow sclerites forming a low arch across the distal edge of the operculum where they are joined. Terminal diaphragms and intramural buds not observed.

Eleozooids (Figs 148, 150, 152–153) numerous, scattered;

small, frontally elongate, about twice as long as wide, a little longer and wider than the autozooids; frontal wall occupying about half of the frontal surface, pseudopores circular and present in about the same density as in the autozooids. Aperture elongate, about twice as long as wide, attaining maximum width close to the hinge line. Rostrum (Fig. 153) long and narrow; in some eleozooids flat, but in most well raised distally, standing above the colony surface by as much as 0·3 mm, so that plane of aperture is inclined by up to 60° to the colony surface, and often with a terminal hook directed proximally. Opercula observed in situ only in overgrown zooids; inner surface of displaced opercula seemingly with marginal sclerites. Apparent intramurally budded eleozooids have thickened rostra and shortened apertures.

Kenozooids occasionally present.

Gonozooids (Fig. 154) present in paratype (VH 10502), frontally almost twice as long as wide, the bulbous distal part being ovoidal or pear-shaped. Ooeciopore (Fig. 153) variably transversely elongate, the ooeciostome sometimes reflexed proximally. Atrial ring not observed.
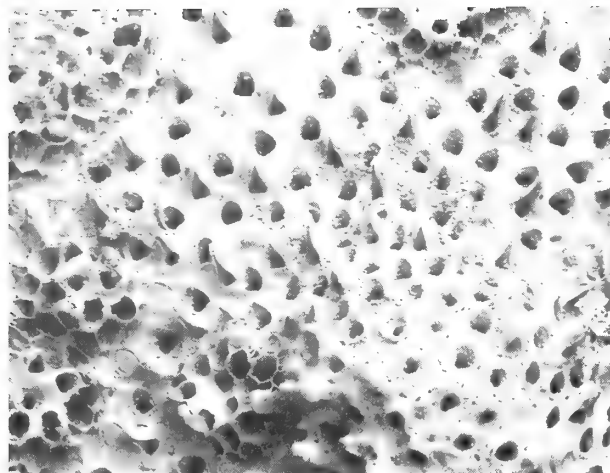
MEASUREMENTS.
autozooids (10 zooids from holotype VH 10427)
frontal length: mean = 0·44 mm; SD = 0·038 mm;
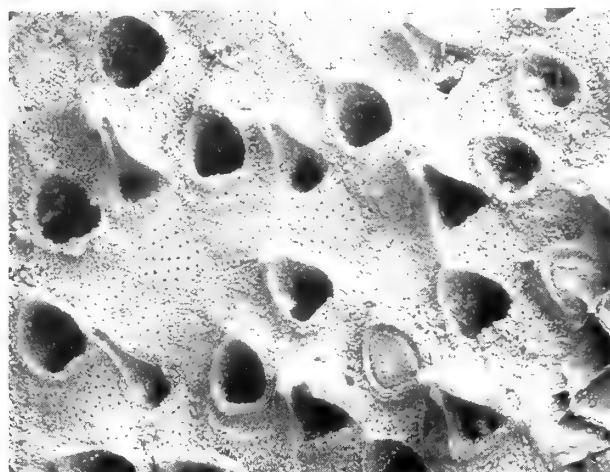CV = 8·7; range = 0·38–0·53 mm
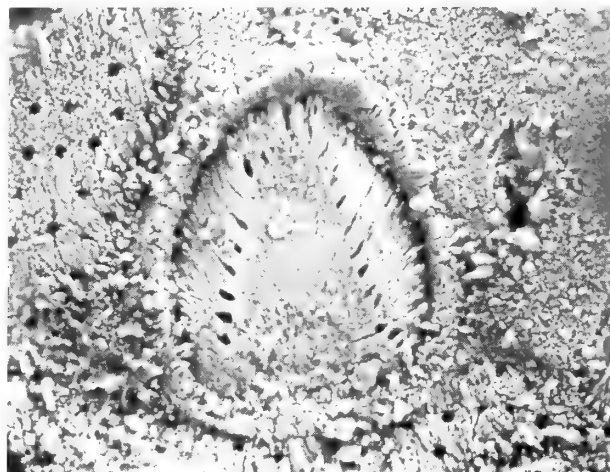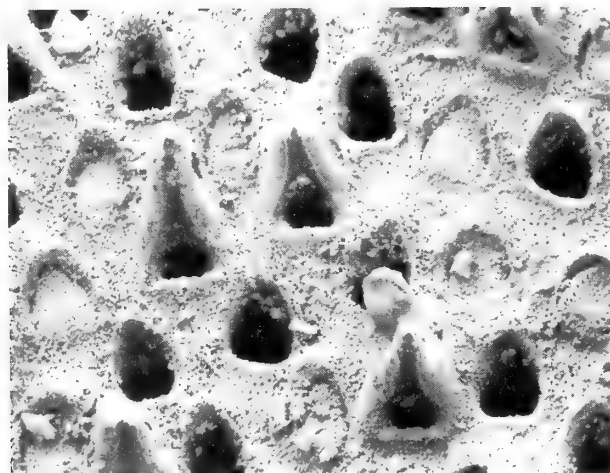frontal width: mean = 0·22 mm; SD = 0·012 mm;
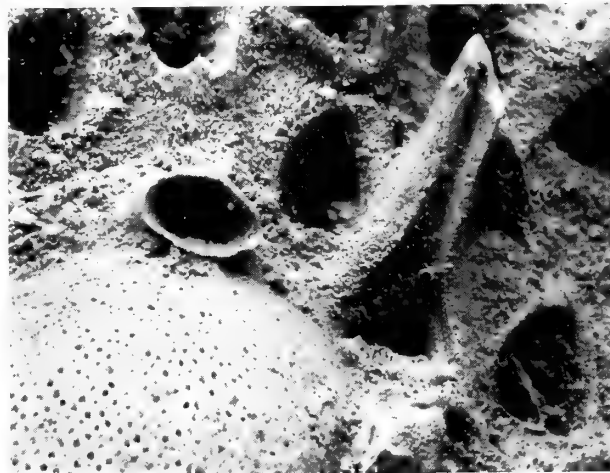
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Figs 148–153 *Reptomultelea acclivata* sp. nov. 148–151, VH 10427, holotype, Lower Cenomanian, Mülheim-Broich, Westfalia, Germany; 148, colony surface showing prominent eleozooids and overgrowths, × 22; 149, small overgrowth, × 40; 150, autozooids and eleozooids, × 55; 151, autozooidal operculum, × 250. 152–153, VH 10502, Lower Cenomanian, Mülheim-Broich; 152, autozooids and eleozooids with distally-raised rostra, × 62; 153, ooeciopore and an eleozooid with long, raised rostrum, × 115.

CV = 5·6; range = 0·21–0·24 mm

apertural length: mean = 0·17 mm; SD = 0·011 mm; CV = 6·7; range = 0·15–0·18 mm

apertural width: mean = 0·15 mm; SD = 0·007 mm; CV = 5·0; range = 0·14–0·15 mm

eleozooids (9 zooids from holotype VH 10427)

frontal length: mean = 0·48 mm; SD = 0·029 mm; CV = 6·1; range = 0·44–0·53 mm

frontal width: mean = 0·24 mm; SD = 0·020 mm; CV = 8·2; range = 0·21–0·27 mm

apertural length: mean = 0·28 mm; SD = 0·055 mm; CV = 19·6; range = 0·21–0·38 mm

apertural width: mean = 0·14 mm; SD = 0·016 mm; CV = 11·5; range = 0·11–0·15 mm

[nb. apertural length measured in the plane of the aperture, i.e. obliquely to the colony surface]

gonozooid (6 zooids from holotype VH 10427)

frontal length: mean = 1·50 mm; SD = 0·056 mm; CV = 3·7; range = 1·44–1·59 mm

distal frontal wall length: mean = 1·30 mm; SD = 0·044 mm; CV = 3·4; range = 1·25–1·35 mm

frontal width: mean = 0·84 mm; SD = 0·046 mm; CV = 5·5; range = 0·80–0·90 mm

ooeciopore length: mean = 0·08 mm; SD = 0·006 mm; CV = 7·9; range = 0·08–0·09 mm

ooeciopore width: mean = 0·14 mm; SD = 0·028 mm; CV = 21·1; range = 0·11–0·17 mm

REMARKS. This new species resembles *Reptomultelea*

Fig. 154 *Reptomultelea acclivata* sp. nov., VH 10502, Lower Cenomanian, Mülheim-Broich, Westfalia, Germany, gonozooid, × 70.

sarthacensis (d'Orbigny) and *R. parvula* sp. nov., with which it co-occurs at Mülheim. However, it differs in having abundant eleozooids with distally raised rostra, causing the plane of the aperture to be at a considerable angle to the colony surface and the colony to have a spiny appearance. In well-preserved specimens the distal ends of the rostra are slightly hooked, a feature unique to *R. acclivata* among melicerititids. Autozooid apertures are less elongate than in *R. sarthacensis* and larger than in *R. parvula*.

The holotype colony evidently encrusted a fragment of a dendroid cyclostome, grew free beyond its initial substratum (as with many other colonies of *Reptomultelea* spp. from Mülheim), and incorporated secondary substrates, including an onychocellid cheilostome bryozoan, into its base.

DISTRIBUTION. Lower Cenomanian of Mülheim, Westfalia, Germany.

Reptomultelea auris sp. nov.   Figs 155–162

MATERIAL. Holotype: BMNH D46049, Turonian, *lata* Zone, Ballard Point, Dorset, England, A.W. Rowe Collection.

Paratypes: BMNH D46048, D46052, same details as holotype. D43694, [Coniacian], *M. cortestudinarium* Zone, Seaford Head, Sussex, England, A.W. Rowe Colln. D46027, Turonian, *planus* Zone, White Nothe, Dorset, England, A.W. Rowe Colln. BZ 1005–6, Turonian, *planus* Zone Chalk, Tilleul Beach, Seine Maritime, France, Taylor and Hammond Colln, 1985. BZ 1007, Coniacian, Craie á *M. normanniae*, above Tilleul No. 3 Hardground (see Kennedy and Juignet, 1974), Etretat, Seine Maritime.

NAME. Auris, Latin for ear, with reference to the paired kenozooids which resemble ears on either side of the autozooidal aperture.

DESCRIPTION. Colony unilamellar or multilamellar, each layer about 0·3 mm thick, generally (?always) cavariiform with tubular branches 5–10 mm in diameter, up to 40 mm in maximum observed length, flexuous and occasionally bifurcating; basal lamina on inside of tubes with transverse undulations, apparently growing freely of a substratum. Overgrowths (Fig. 158) originate by intrazooecial fission; pseudoancestrula an autozooid, aperture depressed, small, about 0·11–0·12 mm long by 0·08 mm wide, surrounded by approximately 6 periancestrular buds initiating a secondary zone of astogenetic change of increasing zooid size. Organization fixed-walled. Zooidal apertures arranged roughly in quincunx away from overgrowth origins and anastomoses.

Autozooids (Figs 155–156, 159, 161) of large size, frontally elongate, usually a little over twice as long as wide, subhexagonal or subrhomboidal in outline, subacuminate distally; frontal wall convex, pseudopores circular; boundary wall salient. Aperture (Fig. 160) of moderate size, longitudinally elongate, on average 1·1–1·2 × longer than wide, attaining maximum width just distal to the hinge line, arched distally; apertural rim narrow; apertural shelf moderately wide distally, tapering proximally; hinge line bowed, raised slightly so that plane of aperture faces distally. Operculum (Figs 157, 162) often preserved in-situ, convex; pseudopores slightly radially elongate, numbering about 20, arranged close to and parallel with the distal edge of the operculum. Terminal
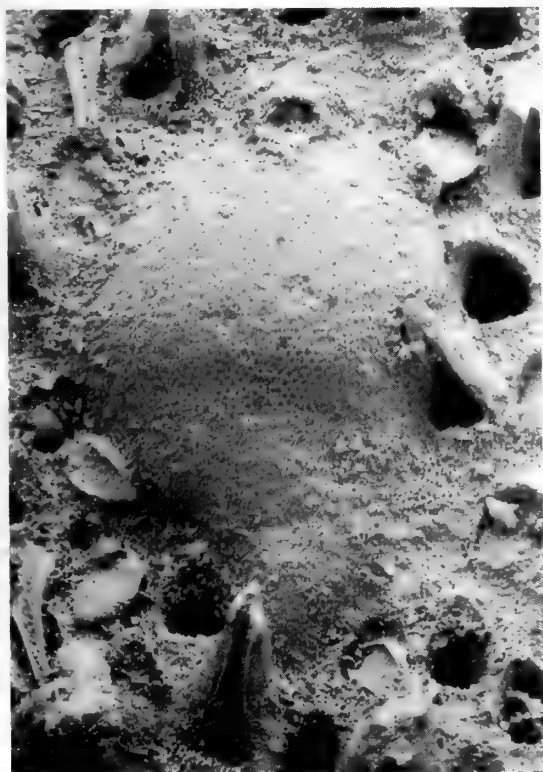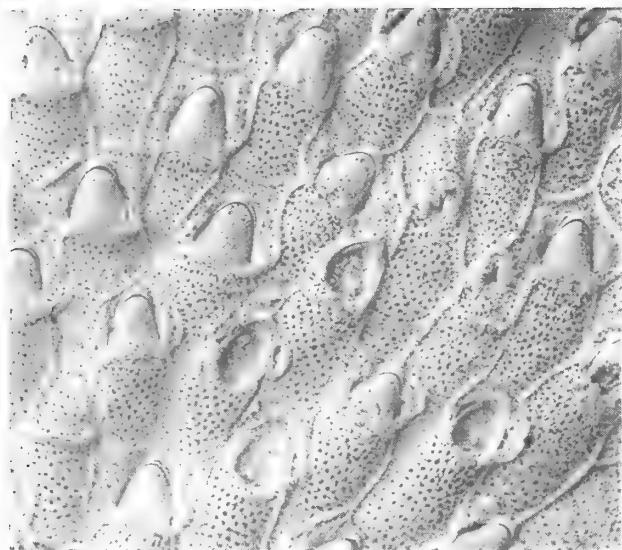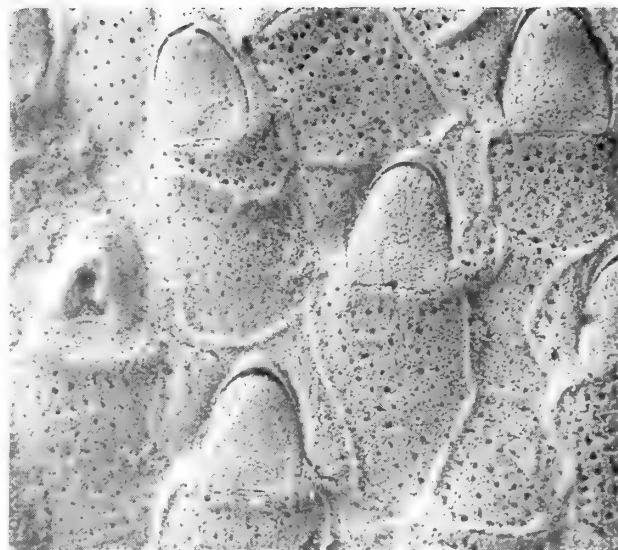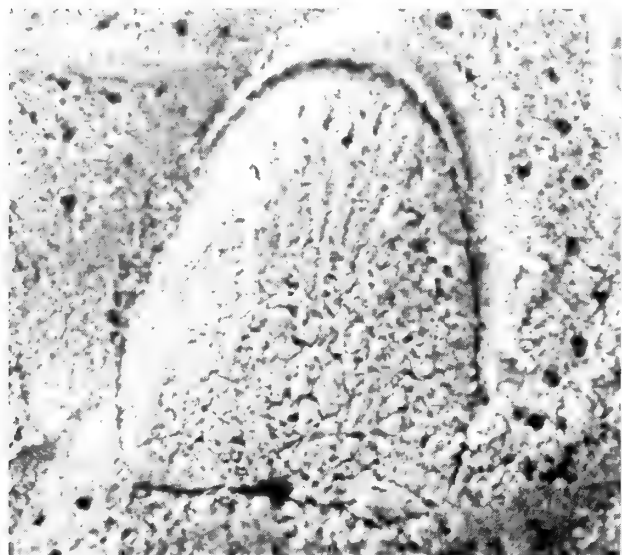
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Figs 155–158   *Reptomultelea auris* sp. nov., BMNH D46049, holotype, Turonian, *lata* Zone, Ballard Point, Dorset, England; 155, autozooids, eleozooids and kenozooids, × 35; 156, operculate autozooids, kenozooids, intramural eleozooid (left), and evidence of regeneration after damage in upper left autozooid, × 72; 157, autozooidal operculum, × 240; 158, overgrowth origin, × 56.

diaphragms not observed. Intramurally budded eleozooids (Fig. 156) common, apertures trifoliate like those of primary eleozooids, elevated distally so that plane of aperture faces proximally.

Kenozooids (Figs 155–156) abundant, small, commonly paired on either side of the autozooidal apertures and semi-circular or crescent-shaped in outline.

Eleozooids (Fig. 161) infrequent, scattered, frontally elongate, typically slightly longer but narrower than the autozooids, narrow and pointed distally. Aperture small, longitudinally elongate, trifoliate in outline, about twice as long as wide, considerably shorter and narrower than autozooidal apertures; apertural rim moderately raised. Opercula not observed. Intramural buds unknown.

Gonozooids known from a single broken example which is missing the proximal part; frontal shape apparently subcircular. Ooeciopore transversely elliptical, slightly more than 2 × wider than long. Atrial ring present.

MEASUREMENTS.
autozooids (10 zooids with in-situ opercula from holotype BMNH D46049)

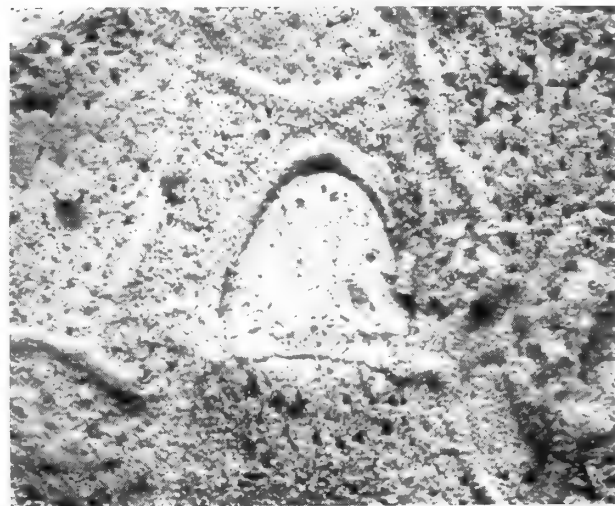|	
frontal length:	mean = 0·66 mm; SD = 0·069 mm; CV = 10·4; range = 0·54–0·78 mm
frontal width:	mean = 0·28 mm; SD = 0·025 mm; CV = 8·7; range = 0·26–0·33 mm
apertural length:	mean = 0·20 mm; SD = 0·008 mm; CV = 3·8; range = 0·20–0·21 mm
apertural width:	mean = 0·17 mm; SD = 0·011 mm; CV = 6·1; range = 0·15–0·18 mm
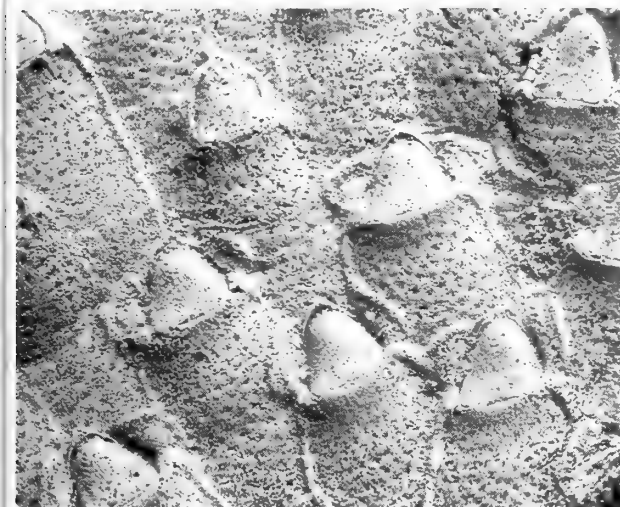
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Figs 159–162 *Reptomultelea auris* sp. nov., 159, BZ 1005, Turonian, *planus* Zone Chalk, Tilleul Beach, Seine Maritime, France, operculate autozooids with small kenozooids lateral to the opercula, × 82. 160–162, BMNH D46049, holotype, Turonian, *lata* Zone, Ballard Point, Dorset, England; 160, autozooidal aperture, × 182; 161, autozooids and primary eleozooid, × 65; 162, autozooidal operculum bordered distally and laterally by a kenozooid, × 125.

eleozooids (3 zooids from holotype BMNH D46049)

frontal length:	range = 0·65–0·87 mm
frontal width:	range = 0·24–0·29 mm
apertural length:	range = 0·12–0·14 mm
apertural width:	range = 0·06–0·08 mm

gonozooid (1 incomplete zooid from BMNH BZ1006)

frontal width:	*ca* 1·13 mm
ooeciopore length:	0·09 mm
ooeciopore width:	0·20 mm

REMARKS. Zooidal dimensions in this new species are similar to *Reptomultelea canui* (Voigt), but *R. auris* differs in having autozooidal apertures more pointed distally and inclined slightly in a distal direction, and also in the presence of common small kenozooids on either side of the autozooidal apertures. These 'ear-like' paired kenozooids are not ubiquitous but are associated with a significant proportion of autozooids in all colonies of *R. auris*. They provide the most

useful means of recognizing the species, being known only from this species among meliceritids.

The cavariiform morphology (*sensu* Brood, 1972) of *R. auris* colonies with free-growing basal laminae suggests loose growth of colonies around, but not directly encrusting, arborescent organisms. Modern colonies of *Schizoporella* and other cheilostomes show a similar morphology when growing loosely around clusters of hydroid stems or other erect substrates.

DISTRIBUTION. Upper Turonian-Coniacian of southern England and northern France.

Reptomultelea betusora nom. nov.   Figs 163–173

?1846 *Diastopora confluens* Reuss: 65, pl. 15, figs 41, 42.
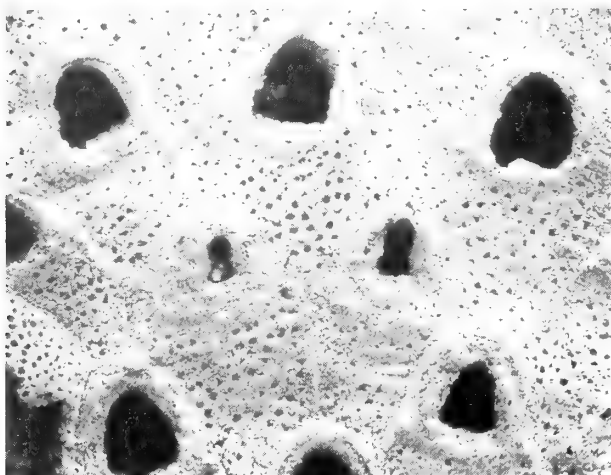 1874 *Diastopora tuberosa* Reuss: 132, pl. II. 25, figs 2 and 3.
 1877 *Diastopora acupunctata* Novák: 99 (partim), pl. 6,
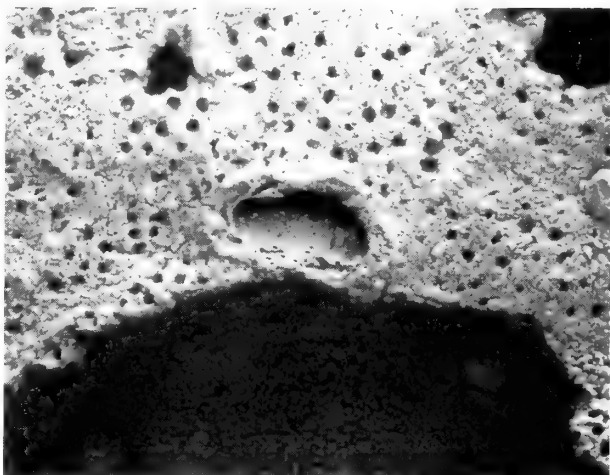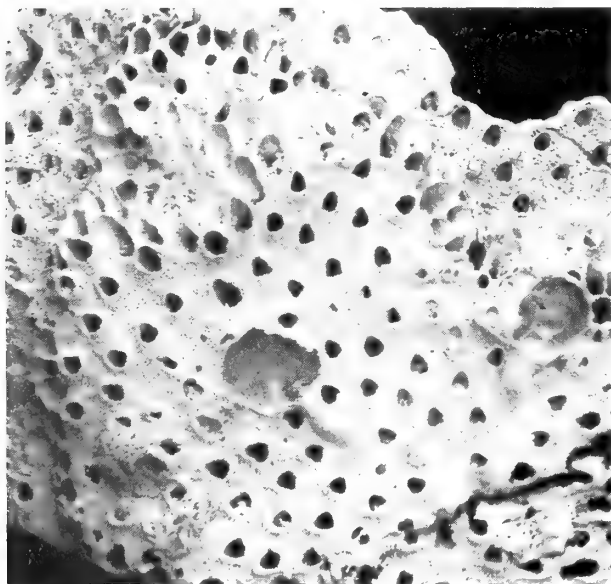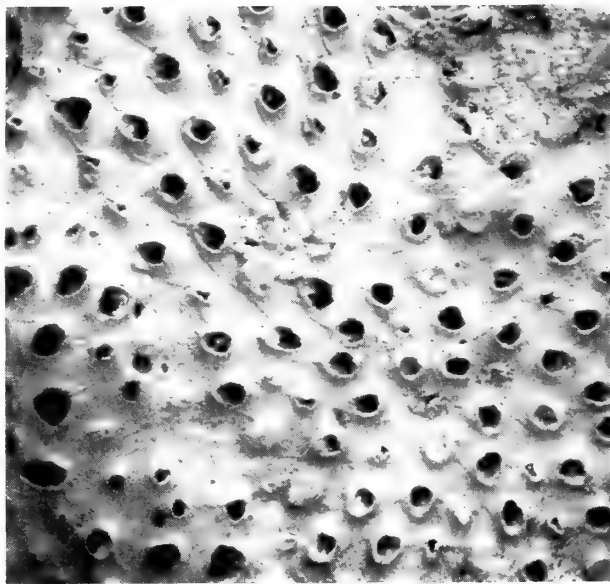
Figs 163–168 *Reptomultelea betusora* nom. nov. 163–164, SMD un-numbered, lectotype, Turonian, Strehlen, Dresden, Germany; 163, pseudoancestrula surrounded by radiating autozooids, × 80; 164, oblique view showing four eleozooids, × 100. 165–167, VH 10436, Upper Cenomanian, *plenus* Zone, Kank, Kutna Hora, Czechoslovakia; 165, autozooids and intramural eleozooids, × 100; 166, ooeciopore, × 180; 167, general view of colony with two broken gonozooids, × 21. 168, BMNH BZ 1000 Coniacian, Craie á *Micraster normanniae*, above Tilleul No. 3 Hardground, Etretat, Seine-Maritime, France, part of large colony, × 22.

figs 2–5, ?figs 6–14 [non fig. 1 = *R. sarthacensis*].
?1877 *Diastopora acupunctata* Novak; Fric: 93, 146, fig. 149.
?1883 *Diastopora acupunctata* Novak; Fric: 81, 124, 125, fig. 104.
?1892 *Semielea acupunctata* (Novák); Pocta: 29, pl. 2, fig. 16.
1899 *Semimultelea acupunctata* (Novák); Gregory: 297.

MATERIAL. Lectotype: SMD un-numbered, the specimen figured here as Figs 163, 164, Turonian, Strehlen, Dresden, Germany. Paralectotypes: SMD un-numbered, 2 specimens in same sample as lectotype.

Other material: VH 10436, Upper Cenomanian, *plenus* Zone, Kank, Kutna Hora, Czechoslovakia. BMNH BZ 999, Cenomanian [*plenus* Zone], Korycaner Schichten, Kamajk, Bohemia, Czechoslovakia, Fric Colln. D58949–50, Turonian, *nodosoides* Zone, Craie á *Inoceramus labiatus*, St Calais road-cutting, Sarthe, France, Taylor & Hammond Colln 1985. BZ 1000–4, Coniacian, Craie á *Micraster normanniae*, above Tilleul No. 3 Hardground (see Kennedy & Juignet, 1974), Etretat, Seine-Maritime, France, Taylor & Hammond Colln 1985.

NAME. An anagram of *tuberosa*.

DESCRIPTION. Colony unilamellar or multilamellar, each layer about 0·35–0·40 mm thick, sometimes growing freely and with a transversely wrinkled basal lamina. Ancestrula not observed. Overgrowths originate by intrazooecial fission; pseudoancestrula (Fig. 163) usually an autozooid (aperture *ca* 0·10 × 0·08 mm diameter), sometimes an eleozooid, surrounded by about 6 daughter buds which initiate a secondary zone of astogenetic change of increasing zooid size. Organization fixed-walled. Zooidal apertures variably arranged, often in irregular quincunx.

Autozooids (Figs 165, 169) medium-sized, frontally elongate, on average about twice as long as wide, often hexagonal or rhomboidal in outline, rounded distally. Frontal wall slightly convex, occupying about two-thirds of the frontal surface, slightly convex; boundary wall salient. Aperture (Fig. 172) small, elongate, about 1·2–1·5 × longer than wide, attaining maximum width about mid-length, moderately rounded distally; apertural rim raised slightly, especially distally; apertural shelf narrow, tapering proximally. Operculum (Fig. 170) seldom preserved in-situ, convex with a crescent of elongate pseudopores. Terminal diaphragms not observed. Intramurally budded eleozooids (Figs 165, 171) frequent, intramural autozooids not seen.

Kenozooids present in varying numbers, sometimes abundant and clustered.

Eleozooids (Figs 164, 169, 171) common; frontal surface generally a little smaller than autozooids but similar in overall proportions, although much narrower distally in the apertural region. Aperture elongate, on average about twice as long as wide, considerably smaller than an autozooidal aperture, inverted T-shaped in outline because of indentation by rostral shelf, often set in a plane oblique to the colony surface and directed proximally. Operculum not observed in-situ.

Gonozooids (Figs 167, 173) known only from specimen VH 10436, which has two, both budded close to the origin of an overgrowth. Frontally relatively small, elongate, about twice

as long as wide, the distal inflated frontal wall emerging from the maternal aperture, initially parallel-sided before dilating and becoming ovoidal. Ooeciopore (Fig. 166) transversely elongate, indented by a proximal hemiseptum. Atrial ring present. Floor of gonozooid has salient outlines of underlying zooids beneath proximal part of dilated frontal wall, smoother distally.

MEASUREMENTS.
autozooids
(10 zooids from VH 10436)

frontal length:	mean = 0·45 mm; SD = 0·042 mm; CV = 9·5; range = 0·39–0·53 mm
frontal width:	mean = 0·21 mm; SD = 0·019 mm; CV = 8·8; range = 0·20–0·24 mm
apertural length:	mean = 0·14 mm; SD = 0·009 mm; CV = 6·9; range = 0·12–0·15 mm
apertural width:	mean = 0·11 mm; SD = 0·008 mm; CV = 7·0; range = 0·11–0·12 mm

(10 zooids from BMNH BZ 1000)

frontal length:	mean = 0·54 mm; SD = 0·040 mm; CV = 7·4; range = 0·50–0·63 mm
frontal width:	mean = 0·28 mm; SD = 0·020 mm; CV = 7·0; range = 0·26–0·32 mm
apertural length:	mean = 0·16 mm; SD = 0·014 mm; CV = 9·1; range = 0·14–0·18 mm
apertural width:	mean = 0·12 mm; SD = 0·009 mm; CV = 7·0; range = 0·11–0·14 mm

eleozooids
(VH 10436)

frontal length:	*ca* 0·35–0·38 mm
frontal width:	*ca* 0·18–0·20 mm
apertural length:	*ca* 0·06–0·08 mm
apertural width:	*ca* 0·05 mm

(5 zooids from BMNH D59329)

|	
frontal length:	mean = 0·50 mm; SD = 0·048 mm; CV = 9·6; range = 0·42–0·54 mm
frontal width:	mean = 0·26 mm; SD = 0·017 mm; CV = 6·6; range = 0·24–0·29 mm
apertural length:	mean = 0·09 mm; SD = 0·024 mm; CV = 26·4; range = 0·06–0·12 mm
apertural width:	mean = 0·04 mm; SD = 0·008 mm; CV = 21·1; range = 0·03–0·05 mm

gonozooids (2 zooids from VH 10436)

frontal length:	1·20–1·29 mm
distal frontal wall length:	0·99–1·11 mm
frontal width:	0·53–0·68 mm
ooeciopore length:	0·06 mm
ooeciopore width:	0·09–0·11 mm

REMARKS. Reassignment of the Reuss (1874) species *tuberosa* from *Diastopora* to *Reptomultelea* makes it a secondary junior homonym of *Reptomultelea tuberosa* d'Orbigny, 1853. Although the latter species, which is the type species of *Reptomultelea*, is a subjective junior synonym of *R. sarthacensis* d'Orbigny, 1853 (see p. 51), a replacement name is nevertheless required for the Reuss species (P.K. Tubbs, ICZN, pers comm. September 1990). This not only avoids potential problems should the synonymy between *R. tuberosa* and *R. sarthacensis* be rejected sometime in the future, but also prevents possible confusion between the species of Reuss and the name of the valid type species of *Reptomultelea*.

169
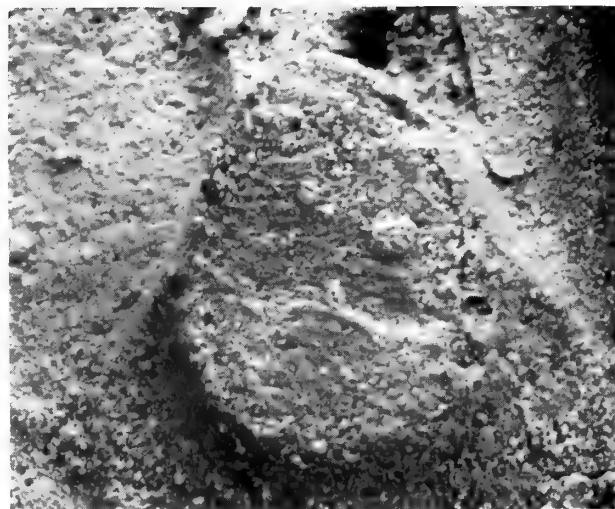
170
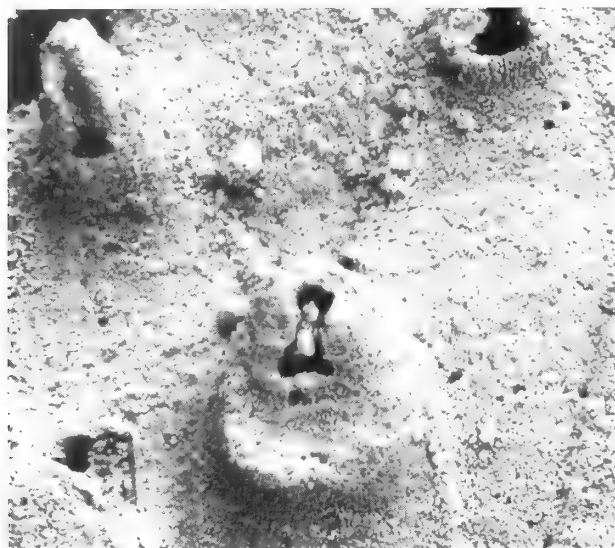
171

172

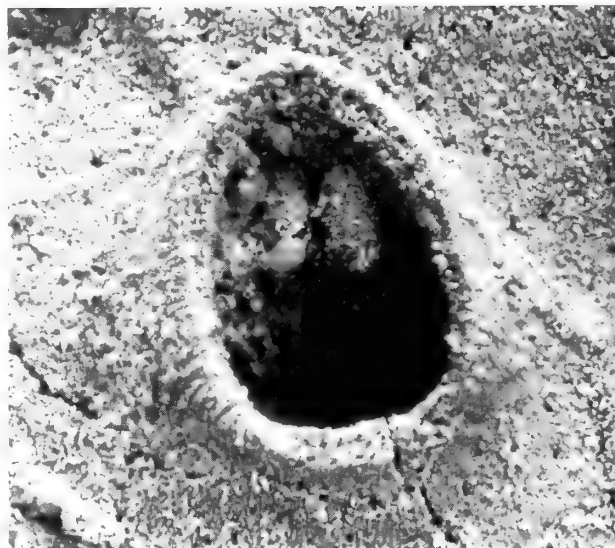**Figs 169–172** *Reptomultelea betusora* nom. nov., BMNH BZ 1000 Coniacian, Craie á *Micraster normanniae*, above Tilleul No. 3 Hardground, Etretat, Seine-Maritime, France; 169, autozooids and eleozooids, × 46; 170, autozooidal operculum, × 270; 171, apertures of primary (top left) and intramural (lower centre) eleozooids, × 160; 172, autozooidal aperture, × 225.

Therefore, *betusora* is here proposed as a nom. nov. for the *tuberosa* of Reuss (1874).

The types of *Diastopora acupunctata* Novák, 1877 were not available for study during a visit to the Narodni Museum, Prague during June 1986· However, judging from Novák's figures and Voigt photocards of this material, some of Novák's specimens belong to *Reptomultelea betusora*, at least one to *Reptomultelea sarthacensis* d'Orbigny, and several others cannot be identified with any reasonable confidence.

Diastopora confluens Reuss, 1846 (non Roemer) is placed tentatively in the synonymy of *R. betusora*. According to Prof. E. Voigt (pers comm., February 1987), the type specimen was destroyed in 1956, but a similar specimen exists in the collections of the Naturhistorisches Museum, Vienna (Voigt photocard 8650).

Reptomultelea betusora is characterized by the presence of small eleozooids of the trifoliozooid type. In this respect it resembles *R. tuberculata* (d'Orbigny, 1853) but the latter species has more elongate autozooidal and eleozooidal apertures.

Specimens of *R. betusora* from the Turonian of Sarthe and from the Coniacian of Etretat have rather larger zooids than Upper Cenomanian material; however, the difference is not considered sufficient to warrant species separation. Colonies are often nodular in form, like those of *R. levinseni* sp. nov. (see p. 77) and *R. sarissata* Gregory (p. 94) which also occur in bryozoan-rich chalks of the Seine Maritime.

DISTRIBUTION. Upper Cenomanian (*plenus* Zone) to Coniacian, Czechoslovakia, Germany and France.
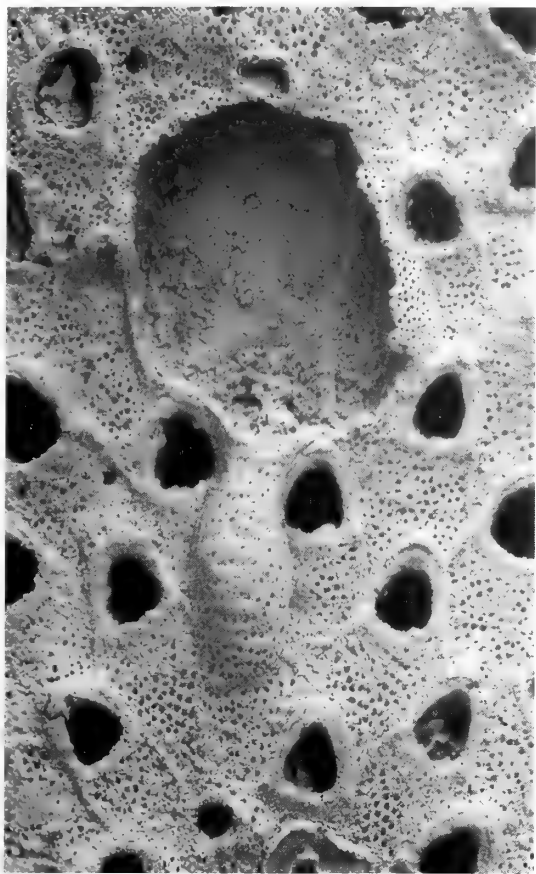
Fig. 173 *Reptomultelea betusora* nom. nov., VH 10436, Upper
Cenomanian, *plenus* Zone, Kank, Kutna Hora, Czechoslovakia,
gonozooid with broken frontal wall, × 75.

Reptelea bituberosa sp. nov.   Figs 174–180

1899   *Reptomultelea tuberosa* d'Orbigny; Gregory: 320, fig.
37.

MATERIAL. Holotype: BMNH 36746, 'Albian, Upper
Greensand', Ventnor, Isle of Wight, England, Norman Col-
lection. This specimen comprises one large piece (70 × 45
mm) in matrix, a coated stub with several small fragments,
and 7 fragments mounted in two cavity slides. Although the
horizon is given as Albian, the close similarity of the matrix to
that of a better localized paratype specimen (D58206) from
the Isle of Wight suggests that the specimen almost certainly
comes from the Lower Cenomanian (*carcitanense* Zone)
Glauconitic Marl (formerly known as the Chloritic Marl).

Paratypes: BMNH D44610, 'Upper Greensand' [? Glauco-
nitic Marl], Niton, Isle of Wight, Ford Colln. BMNH D58206
(2 fragments), Lower Cenomanian, *carcitanense* Zone, basal
conglomerate of the Glauconitic Marl, Rocken End, Isle of
Wight, A. Gale Colln. BMNH D59207, 'Chloritic Marl', St
Catherine's Point, Isle of Wight.

NAME. With reference to the two prominent tubercles at
either end of the hinge line.

DESCRIPTION. Colony encrusting, multilamellar, characteris-
tically large with up to at least 35 layers, each layer about 0·25
mm in thickness. Overgrowths (Fig. 179) develop by eruptive
budding onto the colony surface, often from several closely-
spaced pseudoancestrulae; pseudoancestrula aperture about
0·14 mm long by 0·11 mm wide; peri-pseudoancestrular
zooids usually autozooids, occasionally eleozooids. Ances-
trula not observed. Organization fixed-walled.

Autozooids (Fig. 174) of very large size, frontally elon-
gate, 2–3 × longer than wide, often hexagonal in outline
shape, rather elongate and pointed distally; frontal wall
occupying about half of the frontal surface, flat or slightly
convex with circular pseudopores; zooecial boundary wall
moderately raised. Aperture (Fig. 176) large, very longitu-
dinally elongate, about twice as long as wide, attaining
maximum width approximately mid-length, moderately
rounded distally; apertural rim well-developed, proximally
continuous with prominent tubercles paired at either end of
the hinge line; apertural shelf broad distally, tapering
proximally towards the hinge line; hinge line raised so that
plane of aperture slopes downwards in a distal direction,
with a short median bar running between two hinge teeth.
Operculum (Fig. 175) often preserved in-situ, convex, with
a crescent of slit-shaped pseudopores; sclerite impressions
visible on sediment/cement infilling zooids. Terminal dia-
phragms (Fig. 178) sometimes present, flat, located just
beneath level of apertural rim. Intramurally budded auto-
zooids (Fig. 177) observed but uncommon; in-situ opercula
may occur.

Eleozooids (Figs 179, 180) abundant, scattered; frontal
surface about 2–3 × longer than wide, significantly longer
and a little wider than an autozooid; frontal wall occupying
less than half of the frontal surface, with circular pseudopores
present in a similar density to an autozooid. Aperture elon-
gate, over twice as long as wide, widest at the hinge line,
initially tapering rapidly and then becoming parallel-sided or
slightly spatulate, well-rounded distally; rostrum forming an
extensive platform extending beyond distal end of opercu-
lum; apertural rim less prominent than that of an autozooid,
tubercles absent; hinge line with a wide median bar. Opercula
(Fig. 180) often preserved in-situ, surface convex with a
crescent of slit-shaped pseudopores; distal end of closed
operculum depressed well beneath level of apertural rim;
sclerite impressions visible on sediment/cement infilling zoo-
ids. Intramurally budded eleozooids and autozooids
observed.

Kenozooids (Fig. 174) developed in moderate numbers,
scattered among the autozooids.

Gonozooids present only in the holotype which has two
examples, both occurring in areas of overgrowth anastomosis
and distorted. Frontal wall about twice as long as wide, with a
parallel-sided portion emerging from the maternal aperture,
pear-shaped distally. Ooeciopore poorly-preserved in one
gonozooid, absent in the second.

MEASUREMENTS.
autozooids (10 zooids with in-situ opercula from holotype
BMNH 36746)

frontal length:	mean = 0.78 mm; SD = 0·069 mm;
	CV = 8·9; range = 0·65–0·89 mm
frontal width:	mean = 0·32 mm; SD = 0·038 mm;
	CV = 12·1; range = 0·26–0·38 mm
apertural length:	mean = 0·31 mm; SD = 0·016 mm;
	CV = 5·1; range = 0·29–0·35 mm
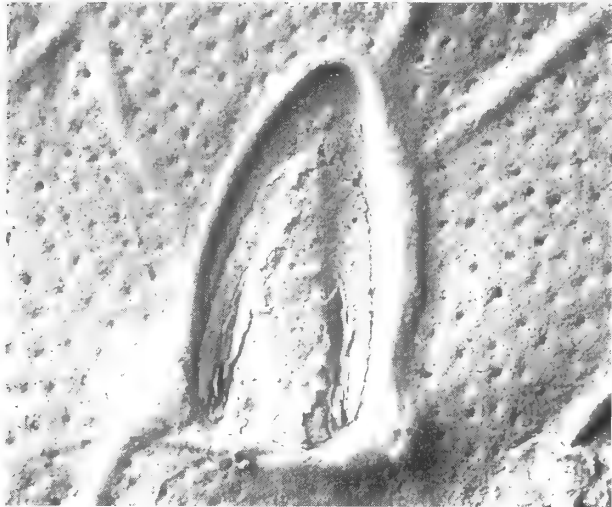
Figs 174–179 *Reptomultelea bituberosa* sp. nov., BMNH 36746, holotype, 'Albian, Upper Greensand' [probably Lower Cenomanian Glauconitic Marl], Ventnor, Isle of Wight, England; 174, autozooids and kenozooids, × 35; 175, autozooidal operculum, × 150; 176, autozooidal aperture with sediment mould of inner surface of operculum, × 150; 177, operculum of intramural autozooid, × 150; 178, autozooidal aperture closed by pseudoporous terminal diaphragm, × 150; 179, overgrowth origin including peri-pseudoancestrular cleozooid, × 50.

apertural width:
mean = 0·16 mm; SD = 0·010 mm;
CV = 6·7; range = 0·15–0·18 mm

eleozooids (8 zooids from holotype BMNH 36746)

frontal length:
mean = 0·92 mm; SD = 0·065 mm;
CV = 7·0; range = 0·83–1·00 mm

frontal width:
mean = 0·36 mm; SD = 0·060 mm;
CV = 16·7; range = 0·30–0·50 mm

apertural length:
mean = 0·54 mm; SD = 0·044 mm;
CV = 8·1; range = 0·48–0·60 mm

apertural width:
mean = 0·24 mm; SD = 0·029 mm;
CV = 12·0; range = 0·21–0·29 mm

gonozooid (one zooid from holotype BMNH 36746)

frontal length: 2·61 mm

distal frontal wall
length: 2·34 mm

frontal wall width: 1·28 mm

REMARKS. Gregory (1899) incorrectly attributed the holotype specimen of this new species to *Reptomultelea tuberosa* d'Orbigny, 1853, a subjective junior synonym of *Reptomultelea sarthacensis* (d'Orbigny, 1851) which is distinguished
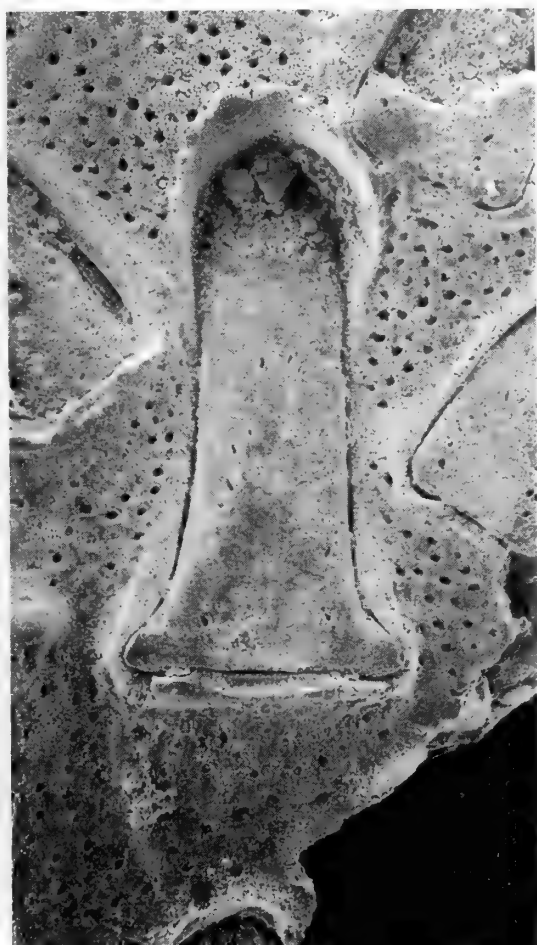

Fig. 180 *Reptomultelea bituberosa* sp. nov., BMNH 36746, holotype, 'Albian, Upper Greensand' [probably Lower Cenomanian Glauconitic Marl], Ventnor, Isle of Wight, England; secondary electron image of coated specimen showing eleozooid with in-situ operculum, × 130.

by the more acute eleozooids (see p. 51). Furthermore, *R. bituberosa* differs from *R. sarthacensis* and other species of *Reptomultelea* in having prominent tubercles at either end of the hinge line in autozooids, and autozooid apertures which are extremely elongate, about twice as long as wide.

DISTRIBUTION. Lower Cenomanian, Glauconitic Marl (*carcitanense* Zone) of the Isle of Wight.

Reptomultelea canui (Voigt, 1924)   Figs 181–183, 185–190

1924   *Semimultelea canui* Voigt: 167, pl. 4, figs 12–13.

MATERIAL. Type: Although the type material of this species was destroyed during World War 2, the unequivocal identity of the species means that it is not necessary to select a neotype.

Other material: BMNH D39514, D39518 (2 pieces), Santonian, Gr. Bülten, Peine, Westfalia, Germany. VH 10305, Lower Santonian, Vallstedt, Westfalia, Germany.

DESCRIPTION. Colony multilamellar, each layer about 0·5 mm thick, the basal surface of the colony sometimes growing free from the original substrate of encrustation and incorporating secondary substrates (Figs 181–183). Overgrowth origins depressed; pseudoancestrula an autozooid, an eleozooid or a kenozooid, surrounded by 6–7 radiating buds (presumably produced by intrazooecial fission) initiating a secondary zone of astogenetic change of increasing zooid size. Organization fixed-walled. Zooidal apertures arranged in quincunx except where disrupted near overgrowth origins and anastomoses.

Autozooids (Figs 185, 188) of medium size, frontally elongate, almost twice as long as wide, rhomboidal in outline, well-rounded distally; frontal wall gently convex, pseudopores subcircular; boundary wall salient. Aperture (Fig. 187) small, usually longitudinally elongate, up to 1·2 × longer than wide, attaining maximum width about mid-length, well-rounded distally; apertural rim raised, continuous with zooidal boundary wall, thickened and prominent at proximo-lateral corners of apertures; apertural shelf narrow; hinge line bowed. Operculum (Fig. 186) often preserved in-situ (especially in older zooids exposed by exfoliating an overlying layer of zooids), convex; pseudopores radially elongate, arranged in an irregular crescent and numbering about 18–20· Terminal diaphragms (Fig. 187) often present at a level just proximal to the apertural shelf, pseudopores not evident (?absent) in most, abundant in some. Intramurally budded eleozooids common, apertures (Fig. 190) of very similar size and shape to primary eleozooids; intramurally budded autozooids not observed.

Kenozooids infrequent.

Eleozooids (Figs 185, 188) moderately abundant, frontally elongate, about the same length and width as the autozooids but more pointed distally. Aperture (Fig. 189) elongate, about twice as long as wide, narrow arch-shaped, attaining maximum width about mid-length; apertural rim prominent distally. Opercula not observed in-situ. Intramural buds not seen.

Gonozooids unknown.

MEASUREMENTS.

autozooids (10 zooids from VH 10305)

frontal length: mean = 0·58 mm; SD = 0·054 mm;
CV = 9·4; range = 0·51–0·71 mm
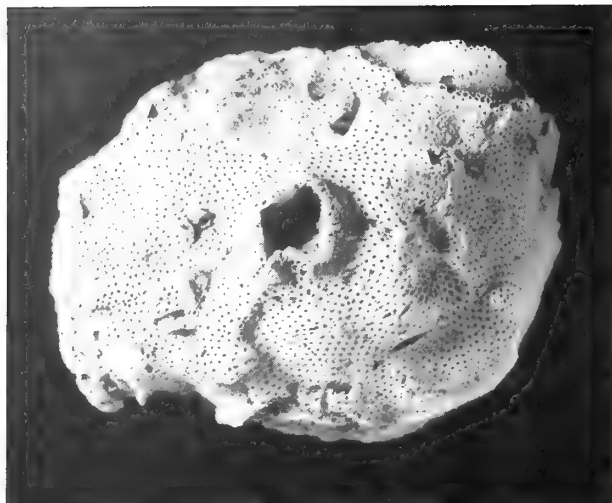
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Figs 181–184 *Reptomultelea* spp., photographs of colonies. 181–183, *R. canui* (Voigt, 1924), VH 10305, Lower Santonian, Vallstedt, Westfalia, 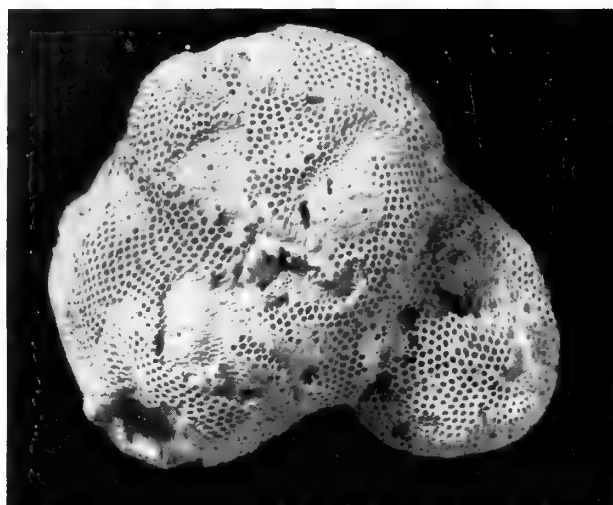Germany, × 2·9; 181, upper side of the colony showing chimney-like growth around an unpreserved object; 182, profile; 183, underside showing original substrate (centre), two secondary substrates (lower right), and free colony growth. 184, *R. goldfussi* sp. nov., EM RE 551.763.31.A745/1, holotype, Cenomanian, Essen, Westfalia, Germany, worn upper surface of colony, × 3·3.

frontal width:	mean = 0·30 mm; SD = 0·023 mm; CV = 7·8; range = 0·27–0·32 mm
apertural length:	mean = 0·17 mm; SD = 0·010 mm; CV = 6·0; range = 0·15–0·18 mm
apertural width:	mean = 0·15 mm; SD = 0·007 mm; CV = 4·7; range = 0·15–0·17 mm

eleozooids (5 zooids from VH 10305)

frontal length:	range = 0·56–0·60 mm
frontal width:	range = 0·30–0·33 mm
apertural length:	range = 0·12–0·15 mm
apertural width:	range = 0·06–0·08 mm

REMARKS. *Reptomultelea canui* co-occurs with the commoner *R. polytaxis* (Voigt, 1924) in the Santonian of Westfalia and can be distinguished from the latter by its larger autozooids and less numerous kenozooids. The combination of well-rounded autozooidal apertures and narrow arch-shaped eleozooidal apertures can be used to recognize *R. canui* among other species of *Reptomultelea*.

DISTRIBUTION. Santonian of Westfalia, Germany.

Reptomultelea convexa sp. nov.   Figs 191–196

MATERIAL. Holotype: VH 10467, Turonian (?), Chenu, between Le Mans and Tours, Sarthe, France, collected by G. Breton.

Paratypes: VH 10443, 10444, 10550 (8 fragments), Turonian, Bois de Gareau, near Ecommoi, Sarthe, France.
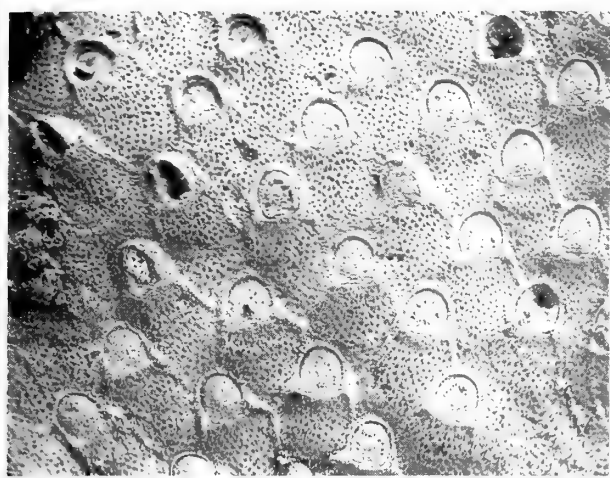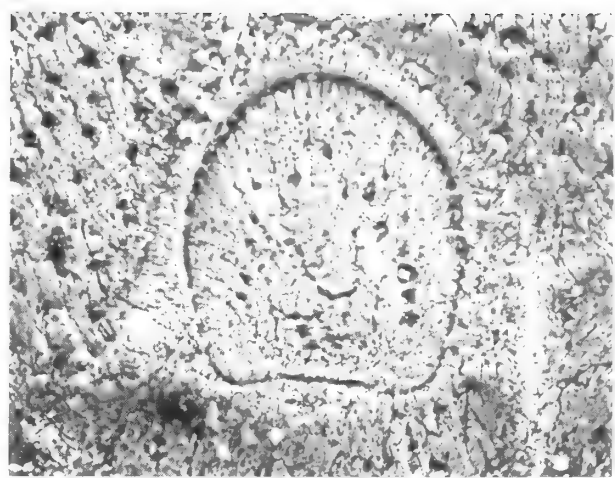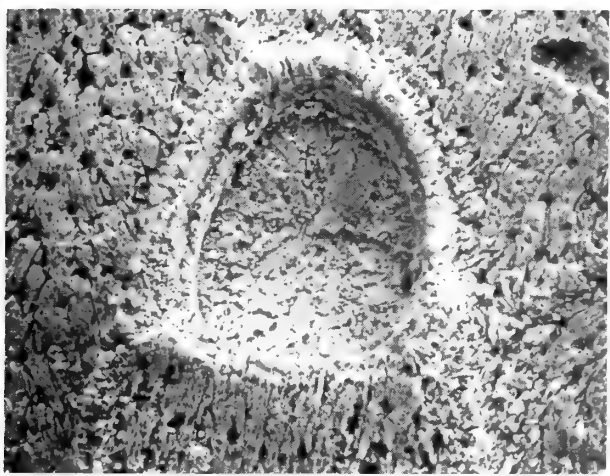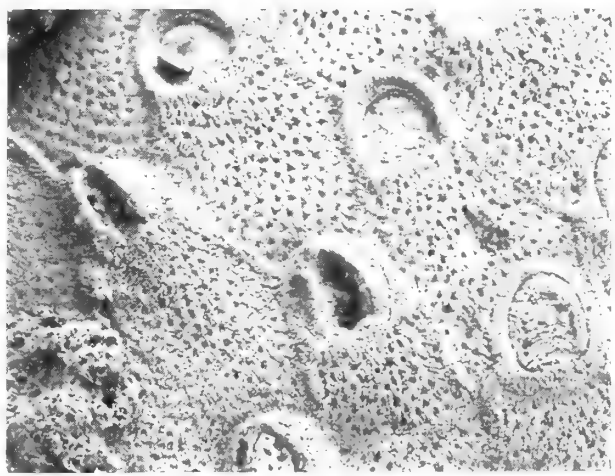
Figs 185–190 *Reptomultelea canui* (Voigt, 1924), VH 10305, Lower Santonian, Vallstedt, Westfalia, Germany; 185, autozooids and eleozooids, × 40; 186, autozooidal operculum, × 300; 187, autozooidal aperture closed by terminal diaphragm, × 250; 188, autozooids and eleozooids, × 85; 189, primary eleozooid aperture, × 250; 190, intramural eleozooid aperture, × 250.

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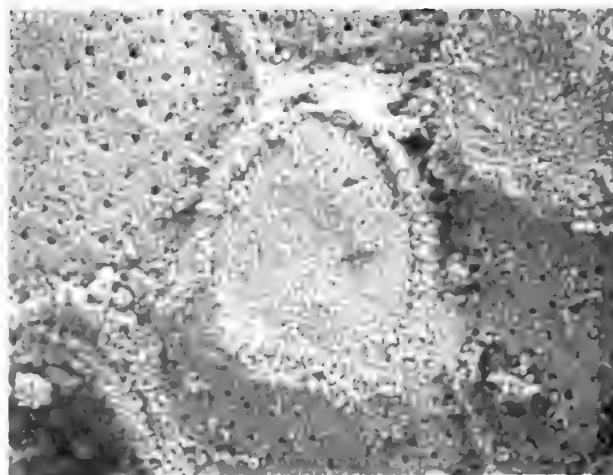
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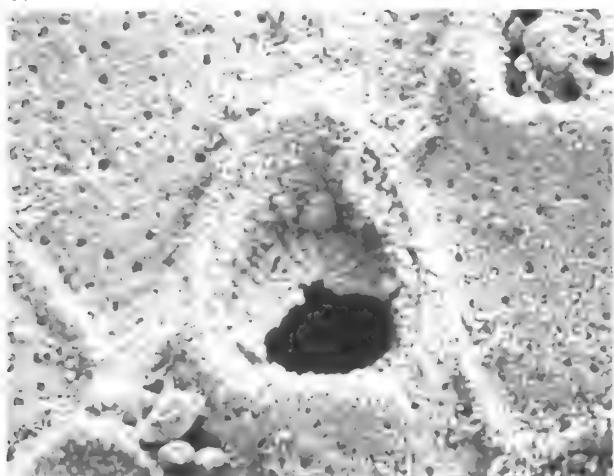
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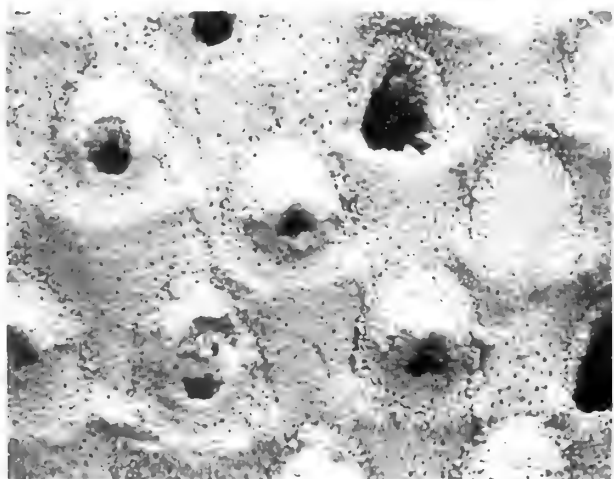
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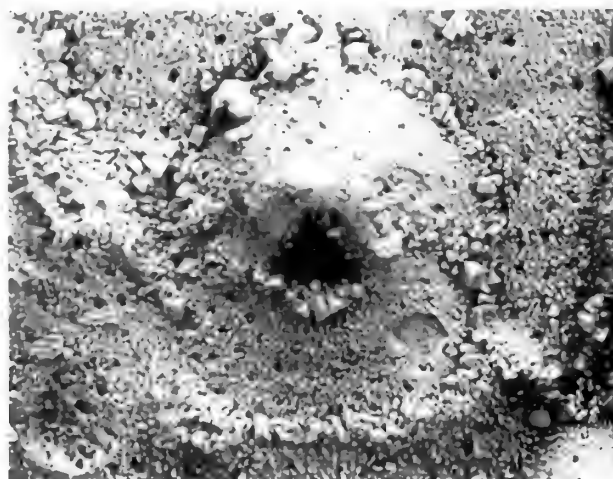
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Figs 191–196 *Reptomultelea convexa* sp. nov. 191–193, VH 10467, holotype, Turonian (?), Chenu, between Le Mans and Tours, Sarthe, France; 191, autozooids and eleozooids, × 42; 192, autozooidal operculum, × 200; 193, autozooidal aperture with broken terminal diaphragm, × 200. 194–196, Turonian, Bois de Gareau, near Ecommoi, Sarthe, France. 194, VH 10444, partly-formed, broken gonozooid (upper left) and overgrowth (upper right), × 33. 195–196, VH 10443; 195, intramural eleozooids and autozooids, × 95; 196, aperture of intramural eleozooid, × 200.

NAME. With reference to the marked convexity of the distal part of the frontal wall.

DESCRIPTION. Colony unilamellar or multilamellar, each layer between 0·23 and 0·30 mm thick, often cavariiform and generally with a free-growing, undulose basal lamina. Overgrowths (Fig. 194) originate through intrazooecial fission. Organization fixed-walled. Apertures arranged roughly in quincunx.

Autozooids (Figs 191, 195) medium-sized, frontally elongate, less than twice as long as wide, usually subhexagonal or subrhomboidal in outline, subrounded distally; frontal wall convex, especially close to the hinge line; boundary wall salient. Aperture (Fig. 193) of moderate size, occupying about a third of the frontal surface, longitudinally elongate, about 1·2–1·3 × longer than wide, arched distally, attaining maximum width about mid-length (or a little proximally of mid-length); apertural rim slightly raised; hinge line poorly preserved in all available specimens; apertural shelf conspicuous, wide to moderately wide, tapering proximally. Operculum (Fig. 192) convex; pseudopores not visible in poorly preserved specimens. Intramurally budded eleozooids common; aperture often cowl-like, directed proximally (Fig. 190).

Kenozooids infrequent.

Eleozooids (Figs 185, 188) common, often clustered in groups of 2 or 3, frontally elongate, less than twice as long as wide and smaller than the autozooids, pointed distally. Aperture (Fig. 189) of small size, trifoliate, about twice as long as wide. Opercula not observed. Intramurally budded eleozooids apparently present, distinguished from 'non-regenerated' eleozooids by proximal inclination of apertural plane.

Gonozooids known from one complete and one broken example (Fig. 194). Frontally of small size, elongate, over twice as long as wide, a parallel-sided tube of variable length emerging from the maternal aperture and dilating into a subcircular distal portion. Ooeciopore transversely elongate, twice as wide as long. Atrial ring not observed.

MEASUREMENTS.

autozooids (10 zooids from holotype VH 10467)

frontal length:	mean = 0·55 mm; SD = 0·053 mm; CV = 9·6; range = 0·48–0·62 mm
frontal width:	mean = 0·33 mm; SD = 0·017 mm; CV = 5·0; range = 0·30–0·35 mm
apertural length:	mean = 0·20 mm; SD = 0·009 mm; CV = 4·3; range = 0·18–0·21 mm
apertural width:	mean = 0·16 mm; SD = 0·007 mm; CV = 4·5; range = 0·15–0·17 mm

eleozooids (8 zooids from holotype VH 10467)

frontal length:	mean = 0·49 mm; SD = 0·052 mm; CV = 10·6; range = 0·44–0·57 mm
frontal width:	mean = 0·28 mm; SD = 0·035 mm; CV = 12·4; range = 0·21–0·32 mm
apertural length:	mean = 0·12 mm; SD = 0·019 mm; CV = 16·6; range = 0·09–0·14 mm
apertural width:	mean = 0·06 mm; SD = 0·005 mm; CV = 8·6; range = 0·06–0·08 mm

gonozooids (1 zooid from VH 10550)

frontal length:	1·62 mm
distal frontal wall length:	1·26 mm
frontal width:	0·71 mm
ooeciopore length:	0·08 mm
ooeciopore width:	0·15 mm

REMARKS. This species is represented only by fragmentary specimens which are either cavariiform or free-growing lamellar. The high convexity of the distal frontal wall close to the aperture is particularly characteristic. Eleozooids have trifoliate apertures like those of *Reptomultelea betusora* nom. nov., *R. polytaxis* (Voigt) and *R. auris* sp. nov., but *R. convexa* has much larger autozooids than *R. polytaxis* and is distinguished by its convex frontal walls from all three species.

The intramurally budded eleozooids in the paratypes (Figs 194–196) are more strongly cowled, autozooidal apertures larger and their shelves broader than in the holotype (Figs 191–193). These differences are not considered to warrant species level separation, however, until sufficient material is available to assess species variability.

DISTRIBUTION. Turonian of Sarthe, France.

Reptomultelea dixoni (Lang, 1906)   Figs 197–201

1899   *Reptomultisparsa rowei* Gregory: 121 (partim) [non pl. 7, fig. 1].

1906   *Semimultelea dixoni* Lang: 64, figs 4 and 12.

MATERIAL. Holotype: BMNH D7845, [Coniacian], *cortestudinarium* Zone, Pit No. 32 of Dibley (1900), opposite the Rose and Crown Inn, Kenley, S. of Croydon, Surrey, England, Withers and Chatwin Collection.

Other material: BMNH D3031 (2 fragments), Upper Chalk, Offham Pit, Lewes, Sussex, Capron Colln (originally described as *Reptomultisparsa rowei* Gregory, 1899). BMNH D31844–50 (fragments of one colony), [Turonian], Dunton Green, Sevenoaks, Kent, England, Dibley Colln. BMNH D43660, [Coniacian], *cortestudinarium* Zone, Seaford Head, Sussex, England, Rowe Colln. BMNH D46061, D46066, Turonian, *lata* Zone, White Cliff to the Hooken, Devon, Rowe Colln. BMNH D57505–9, Coniacian, Craie á *M. normanniae*, above Tilleul No. 3 Hardground (see Kennedy & Juignet, 1974), Etretat, Seine Maritime, France, Taylor & Hammond Colln.

DESCRIPTION. Colony unilamellar or multilamellar, each layer about 0·27–0·41 mm thick, occasionally growing freely with an exposed basal lamina. Overgrowths (Fig. 197) originate through intrazooecial fission from one or several closely-spaced parental zooids; pseudoancestrula either an autozooid (aperture 0·15 × 0·12 mm) or a kenozooid, initiating a secondary zone of astogenetic change of increasing zooid size. Organization fixed-walled. Zooidal apertures variably arranged, often irregular.

Autozooids (Figs 198, 199) large, frontally elongate, about 1·6–2 × longer than wide, variable in shape; frontal wall slightly convex, pseudopores apparently small and subcircular; boundary wall salient. Aperture of moderately large size, a little longitudinally elongate, on average 1·1 × longer than wide, attaining maximum width about mid-length, slightly pointed distally; apertural rim raised, drawn to a projecting point distally; apertural shelf narrow, tapering proximally; hinge line short, teeth and bar not clearly visible in the inadequately preserved material available. Operculum (Fig. 200) often preserved in-situ, convex; pseudopores not observed due to poor surface preservation. Terminal diaphragms (Fig. 193) may be present just beneath apertural shelf. Intramural buds not observed.

Kenozooids (Figs 198, 199) common, variable in number, intercalated among other zooids in the normal budding

197
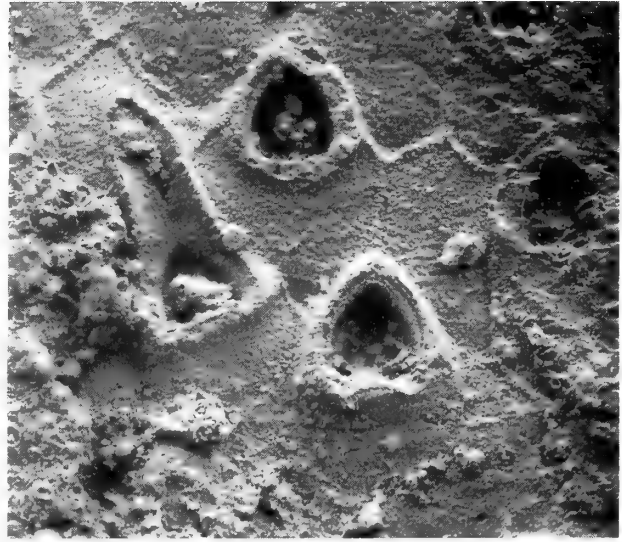
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199

200

Figs 197–200 *Reptomultelea dixoni* (Lang, 1906). 197, BMNH D7845, holotype, [Coniacian], *cortestudinarium* Zone, Kenl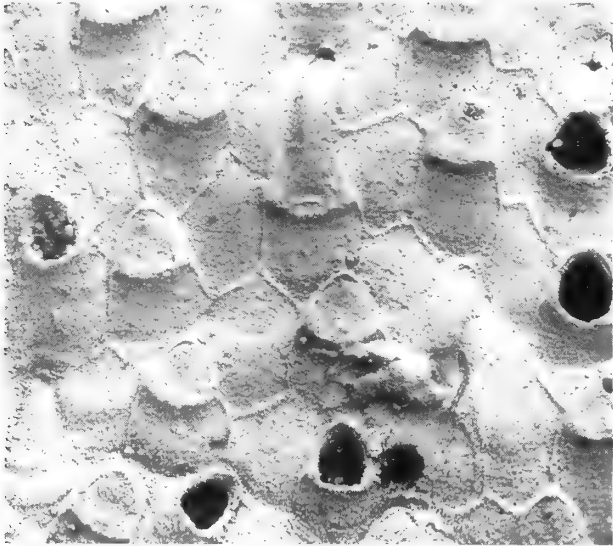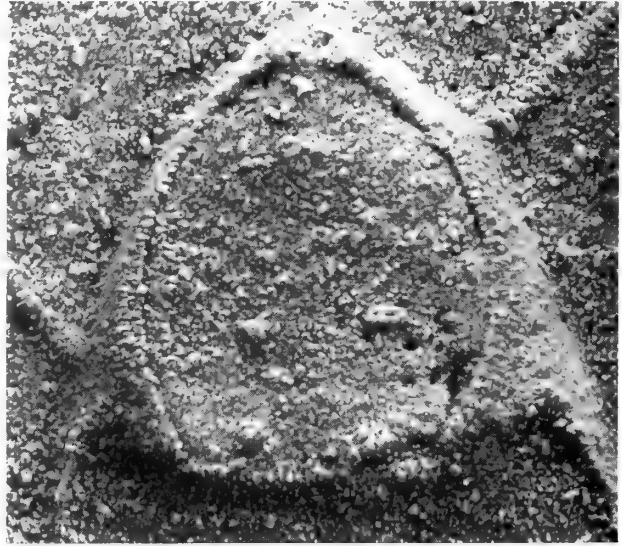ey, Surrey, England, overgrowth origin, × 23. 198, BMNH D31844, [Turonian], Dunton Green, Sevenoaks, Kent, England, autozooids, kenozooids and an eleozooid, × 55. 199–200, BMNH D57506, Coniacian, Craie á *M. normanniae*, Etretat, Seine Maritime, France; 199, autozooids, kenozooids and eleozooids, × 37; 200, autozooidal operculum, × 215.

sequence and also developed at anastomoses between overgrowths; frontally polygonal in outline and invariably shorter and narrower than the autozooids.

Eleozooids (Figs 198, 199, 201) moderately common, frontally elongate, 2–3 × longer than wide, longer but about the same width as the autozooids. Aperture elongate, spatulate, parallel-sided or slightly tapering, widest at the hinge line, rounded distally; rostral shelf extensive, depressed distally. Opercula (Fig. 201) often preserved in-situ; pseudopores not observed due to poor surface preservation. Terminal diaphragms observed. Intramural buds not seen.

Gonozooids unknown.

MEASUREMENTS.
autozooids
(10 zooids from holotype BMNH D7845)

frontal length:	mean = 0·73 mm; SD = 0·073 mm; CV = 10·0; range = 0·62–0·84 mm
frontal width:	mean = 0·41 mm; SD = 0·050 mm; CV = 12·3; range = 0·36–0·50 mm
apertural length:	mean = 0·24 mm; SD = 0·015 mm; CV = 6·3; range = 0·21–0·26 mm
apertural width:	mean = 0·22 mm; SD = 0·014 mm; CV = 6·2; range = 0·20–0·24 mm

(5 zooids from BMNH D57506)

frontal length:	range = 0·62–0·72 mm
frontal width:	range = 0·36–0·41 mm
apertural length:	range = 0·23–0·26 mm
apertural width:	range = 0·20–0·24 mm

eleozooids (5 zooids from BMNH D57506)

frontal length: range = 0·77–1·05 mm
frontal width: range = 0·32–0·42 mm
apertural length: range = 0·38–0·59 mm
apertural width: range = 0·17–0·29 mm

kenozooids (6 zooids from BMNH D57506)
frontal length: range = 0·48–0·60 mm
frontal width: range = 0·32–0·38 mm

REMARKS. The holotype specimen lacks unequivocal eleo-zooids, as noted by Lang (1906) in his original description of *Reptomultelea dixoni* which is based entirely on this specimen. However, eleozooids are present in most other colonies (e.g. Figs 198, 199, 201). Among congeneric species, *R. dixoni* closely resembles *R. sarissata* Gregory, 1899 in the morphology of the eleozooid which has an elongate aperture and is often spatulate. However, although similarly pointed, the autozooidal apertures of *R. dixoni* lack the distal prolongations of *R. sarissata* apertures which give them a distinctive ogee arch-shape (Figs 282, 283).

The proportion of kenozooids to other zooids varies greatly between colonies of this species. In some colonies (e.g. BMNH D31844), kenozooids occupy about the same surface area and are more numerous than autozooids. The high proportion of kenozooids in colonies like this one are unrelated to disturbances in growth caused by anastomoses of overgrowths.

Colonies vary from lamellar to nodular in shape. Specimen BMNH D57505 bioimmures a perished substratum of unknown identity which was roughly cylindrical in outline and ornamented by tubercles.

DISTRIBUTION. Turonian (*lata* Zone)-Coniacian (*cortestudinarium* Zone) of southern England and northern France.

Reptomultelea filiozati (Levinsen, 1912)   Figs 202–208

1912   *Meliceritites filiozati* Levinsen: 34, pl. 6, figs 7–10.
1990   *Reptelea filiozati* (Levinsen); Taylor: fig. 11.2.

MATERIAL. Lectotype (herein designated): ZMC Levinsen Collection M13, 'Middle Senonian', Fécamp, Seine-Maritime, France; the specimen shown in Levinsen's plate 6, figure 7. Paralectotypes: ZMC Levinsen Colln M12, M14–20, same details as lectotype.

Other material: BMNH D54286–7, Coniacian, Fécamp, Voigt Colln. VH un-numbered specimens from same horizon and locality.

DESCRIPTION. Colony unilamellar or multilamellar, each layer about 0·3 mm thick, often becoming free with a transversely wrinkled basal lamina. Overgrowths apparently originate through intrazooecial fission, often from several closely-spaced pseudoancestrulae (Fig. 206); pseudoancestrulae are autozooids with apertures about 0·11 mm long and wide, sometimes operculate (Fig. 207); peri-pseudo-ancestrular zooids number 5–6 and commence a zone of secondary astogenetic change marked by increasing zooid size. Organization fixed-walled. Zooidal apertures arranged roughly in quincunx.

Autozooids (Figs 202, 205) of large size, elongate, on average a little less than twice as long as wide, diamond-shaped, pentagonal, rhomboidal or hexagonal in outline, well-rounded distally; frontal wall gently convex, occupying about two-thirds of the frontal surface; pseudopores small, circular; boundary wall salient, clearly visible. Apertures (Fig. 204) of moderate size, elongate, about 1·25 × longer

Fig. 201 *Reptomultelea dixoni* (Lang, 1906), BMNH D57505, Coniacian, Craie á *M. normanniae*, Etretat, Seine Maritime, France; eleozooid with in-situ operculum, × 105.

than wide, attaining maximum width about mid-length, well-rounded distally; apertural rim slightly raised; apertural shelf narrow, tapering proximally; hinge line with a median bar. Operculum (Fig. 203) often preserved in-situ, slightly convex; pseudopores not clearly visible in studied material. Diaphragms and intramural buds not observed.

Kenozooids (Figs 202, 205) common, especially clustered at anastomoses between overgrowths.

Eleozooids (Figs 202, 206, 208) moderately common, large, frontally elongate, about 2·5–3 × longer than wide, longer but slightly narrower than the autozooids. Aperture elongate, about twice as long as wide and twice the length of an autozooidal aperture, more or less parallel-sided, well-rounded distally with an extensive rostral platform depressed beneath the level of the apertural rim; hinge line with a long median bar. Opercula not observed in-situ. Intramural buds not seen.

Gonozooids unknown.

MEASUREMENTS.
autozooids (10 zooids from lectotype ZMC M13)
frontal length: mean = 0·62 mm; SD = 0·049 mm;
                            CV = 8·0; range = 0·56–0·71 mm
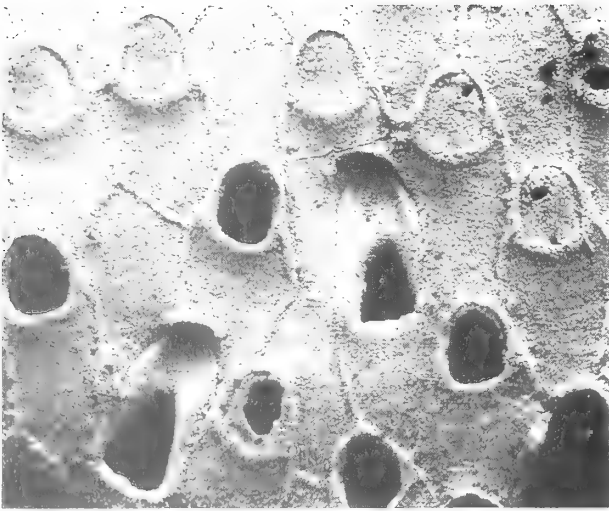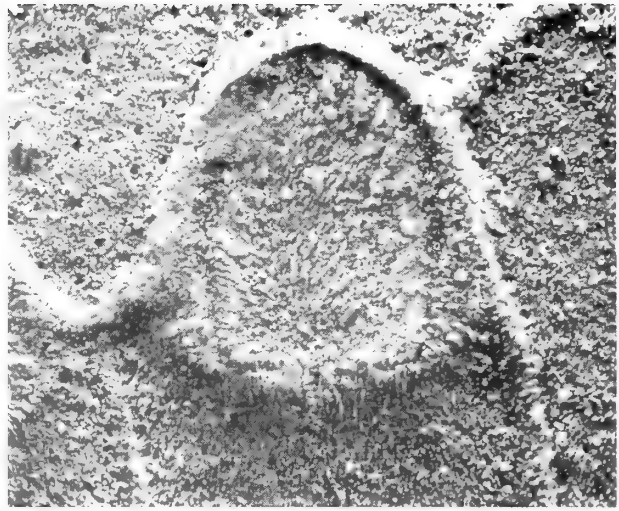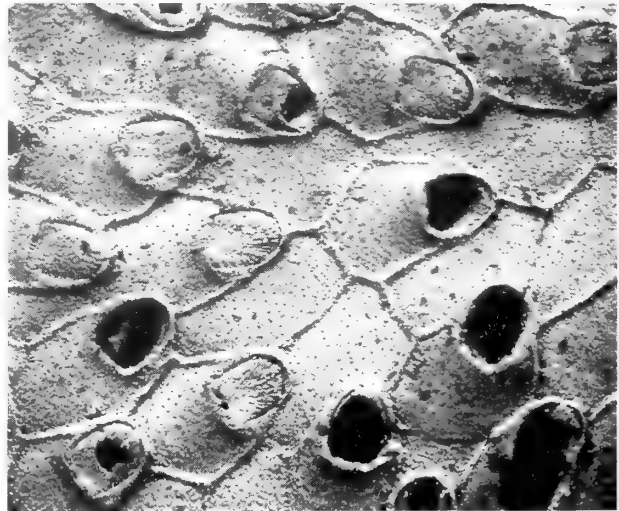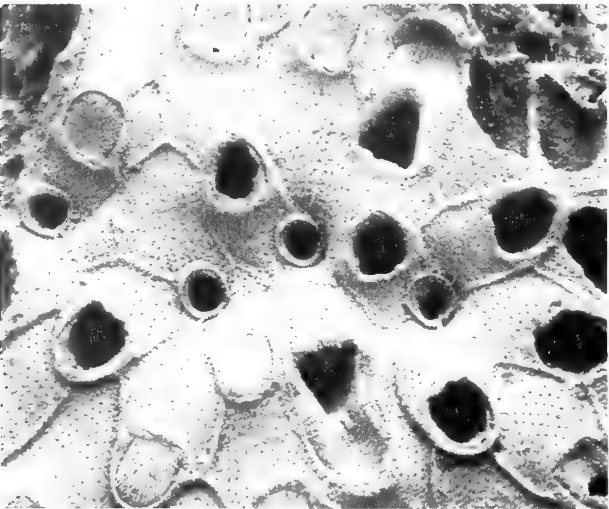
Figs 202–207 *Reptomultelea filtozati* (Levinsen, 1912), 'Middle Senonian', Fécamp, Seine-Maritime, France. 202–204, ZMC Levinsen Colln M12; 202, autozooids, eleozooids and kenozooids, × 55; 203, autozooidal operculum, × 245; 204, autozooidal aperture, × 250. 205–207, ZMC Levinsen Colln M13, lectotype; 205, area of coalescent growth with kenozooids and autozooids, × 55; 206, four closely-spaced pseudoancestrulae surrounded by radiating autozooids, eleozooids and kenozooids, × 55; 207, operculate pseudoancestrula surrounded by five autozooidal buds, × 78.

Fig. 208 *Reptomultelea filiozati* (Levinsen, 1912), ZMC Levinsen Colln M12, Middle Senonian', Fécamp, Seine-Maritime, France; eleozooid, × 155.

frontal width:	mean = 0·34 mm; SD = 0·036 mm; CV = 10·7; range = 0·30–0·42 mm
aperturalength:	mean = 0·20 mm; SD = 0·009 mm; CV = 4·8; range = 0·18–0·21 mm
apertural width:	mean = 0·16 mm; SD = 0·006 mm; CV = 3·9 range = 0·15–0·17 mm

eleozooids (5 zooids from lectotype ZMC M13)

frontal length:	range = 0·68–0·80 mm
frontal width:	range = 0·27–0·30 mm
apertural length:	range = 0·38–0·41 mm
apertural width:	range = 0·17–0·20 mm

REMARKS. The shape of the eleozooidal aperture is very characteristic in *Reptomultelea filiozati* and enables immediate distinction from most other species of the genus. Only *R. pegma* sp. nov. (see p. 85) and *R. scanica* sp. nov. (see p. 96) have similarly broad eleozooidal apertures, but both species are readily distinguished from *R. filiozati* by other means (e.g. *R. pegma* has oblique autozooidal apertures with wide apertural shelves, and *R. scanica* has autozooidal apertures which occupy a significantly greater proportion of the frontal surface than in *R. filiozati*).

According to Prof. E. Voigt, this is a rare species. It is known to occur with certainty only in the Coniacian of the Fécamp area of Seine-Maritime in northern France, although the Voigt Collection in Hamburg contains a possible example (un-numbered) from the Coniacian of Villedieu.

DISTRIBUTION. Coniacian of Seine-Maritime, France.

Reptomultelea goldfussi sp. nov. Figs 184, 209–216

MATERIAL. Holotype: EM RE 551.763.31.A745/1, Cenomanian, Essen, Westfalia, Germany. Paratypes: VH 10426, 10548 (8 fragments), Lower Cenomanian, Mülheim/Ruhr, Westfalia, Germany.

NAME. In honour of Georg August Goldfuss (1782–1848), the first author to describe a meliceritid species, *Ceriopora gracilis* Goldfuss, 1827, later to become the type species of *Meliceritites* Roemer.

DESCRIPTION. Colony (Figs 184, 211) unilamellar or multilamellar, each layer about 0·25–0·35 mm thick, sometimes growing freely of underlying layers and incorporating secondary substrata. Ancestrula not observed. Overgrowths originate through intrazooecial fission, often from several closely-spaced parent zooids; pseudoancestrula (Figs 212, 213) an autozooid which may be occluded by a terminal diaphragm, initiating a secondary zone of astogenetic change of increasing zooid size. Organization fixed-walled. Zooidal apertures arranged in regular quincunx, disrupted close to overgrowth origins.

Autozooids (Figs 209, 212) of moderate size, frontally elongate, about 1·5–2 × longer than wide, rhomboidal in outline, well-rounded distally; frontal wall occupying about half of frontal surface, slightly convex, with circular pseudopores; boundary wall salient, variably prominent. Aperture (Fig. 212) large, usually a little longer than wide, attaining maximum width just proximally of mid-length; apertural rim conspicuous but low, continuous with lateral zooecial boundary wall; apertural shelf rather narrow (less than 0·02 mm wide), tapering to nothing at widest point of aperture; hinge line with median bar and low teeth at either end. Operculum (Figs 210, 220) occasionally preserved in-situ, surface convex; pseudopores elongated parallel to growth direction, scattered across entire surface of operculum. Terminal diaphragms seldom observed, pseudoporous. Intramurally budded autozooids uncommon.

Kenozooids not observed.

Eleozooids not observed, presumed absent.

Gonozooids represented by one example in the holotype colony (Fig. 209); frontal surface slightly longer than wide, becoming triangular in outline soon after emergence of the distal frontal wall from the maternal aperture; margins of distal frontal wall irregular, indented by adjacent autozooids. Ooeciopore very large, about the same width as an autozooid aperture but less than half the length.

MEASUREMENTS.
autozooids
(10 zooids with in-situ opercula from holotype EM RE 551.763.31.A745/1)

| frontal length: | mean = 0·55 mm; SD = 0·051 mm; CV = 9·2; range = 0·48–0·63 mm |
| frontal width: | mean = 0·32 mm; SD = 0·018 mm; CV = 5·5; range = 0·30–0·35 mm |
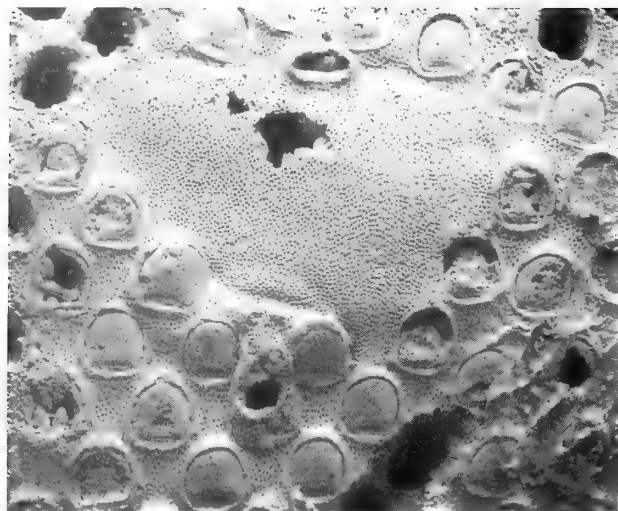
Figs 209–210 *Reptomultelea goldfussi* sp. nov., EM RE 551.763.31.A745/1, holotype, Cenomanian, Essen, Westfalia, Germany; 209, gonozooid and autozooids, × 30; 210, autozooidal operculum, × 150.

apertural length:	mean = 0·26 mm; SD = 0·022 mm; CV = 8·8; range = 0·23–0·30 mm
apertural width:	mean = 0·25 mm; SD = 0·018 mm; CV = 7·2; range = 0·23–0·29 mm

gonozooids
(1 zooid from holotype EM RE 551.763.31.A745/1)

frontal length:	2·03 mm
distal frontal wall length:	1·80 mm
frontal width:	1·80 mm
ooeciopore length:	0·11 mm
ooeciopore width:	0·24 mm

REMARKS. The large and well-rounded autozooidal apertures distinguish *Reptomultelea goldfussi* from other species in the genus. As noted below (p. 91), *R. goldfussi* resembles *R. reedi* sp. nov. but is distinguished most convincingly by the occurrence of pseudopores across the entire surface of the operculum rather than in a crescentic row. The holotype (Figs 209, 210) differs from the paratypes (Figs 211–216) in having somewhat taller and larger autozooidal apertures. These differences may be astogenetic in origin because the paratypes comprise zooids close to overgrowth originations and probably within secondary zones of astogenetic change.

DISTRIBUTION. Lower Cenomanian of Westfalia, Germany.

Reptomultelea levinseni sp. nov.　　　Figs 217–223

MATERIAL. Holotype: BMNH D58930 (2 fragments), Coniacian or basal Santonian, *decipiens* Chalk, Vattetot, Seine Maritime, France, Taylor & Hammond Collection. Paratypes: BMNH D58931 (sample), D59248, D59249, same horizon and locality as holotype. ZMC Levinsen Colln M56, [?Coniacian], Fécamp, Seine Maritime, France; labelled by Levinsen '*Clausimultelea* sp.n.?'.

NAME. For G.M.R. Levinsen, author of the most important work on melicerititid cyclostomes.

DESCRIPTION. Colony generally multilamellar, each layer about 0·26 mm thick and occasionally growing free of underlying layers and with an undulose basal lamina. Ancestrula not observed. Overgrowths originate by intrazooecial fission, often from several clustered parental zooids depressed beneath general level of colony surface; pseudoancestrula an autozooid or a kenozooid budding a ring of daughter zooids, sometimes including a gonozooid (Fig. 221), forming the initial part of a secondary zone of astogenetic change through which zooid size increases. Organization fixed-walled. Zooids arranged roughly in quincunx.

Autozooids (Figs 217, 218) of large size, frontally elongate, about 2–2·5 × longer than wide, generally hexagonal to diamond-shaped in outline, pointed distally; frontal wall occupying more than half of the frontal surface, slightly convex, with circular pseudopores set in elongate depressions; boundary wall well-defined, salient. Aperture (Fig. 219) of moderate size, approximately 1·5 × longer than wide, gothic arch-shaped, pointed distally, attaining maximum width at a point between the hinge line and mid-length; apertural rim well-developed, pointed and raised distally; apertural shelf narrow; hinge line short, with low teeth at either end of a median bar. Operculum (Fig. 220) often preserved in-situ, convex, pseudopores present but number uncertain. terminal diaphragms may be present beneath level of operculum. Intramural buds not observed.

Eleozooids (Figs 217, 218, 223) abundant, scattered; frontal surface about 3–4 × longer than wide, considerably longer than the autozooids but approximately the same width; frontal wall occupying more than half of the frontal surface, slightly convex and with a similar density of pseudopores to the autozooids. Aperture elongate, 2–3·5 × longer than wide, widest a little distally of the hinge line, with a long, narrow rostral area becoming parallel-sided or even very slightly spatulate; rostrum depressed distally; hinge line with a median bar proximal to which is a depressed area; aperture width constricted proximally by wall thickenings which join distally to form the rostral shelf. Operculum (Fig. 223) sometimes preserved in-situ, surface convex, especially distally. Terminal diaphragms and intramural buds not observed.
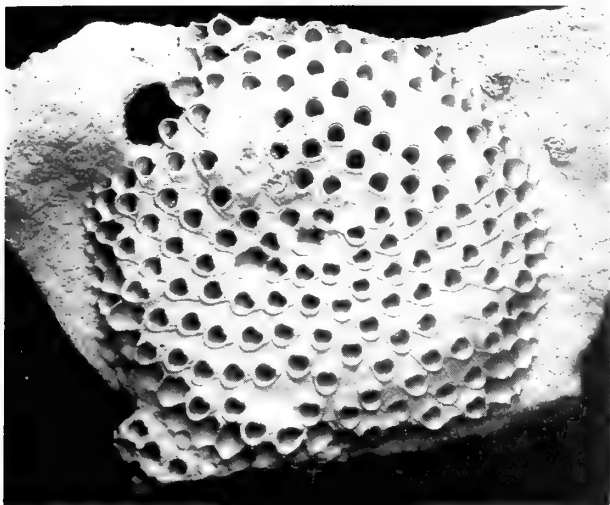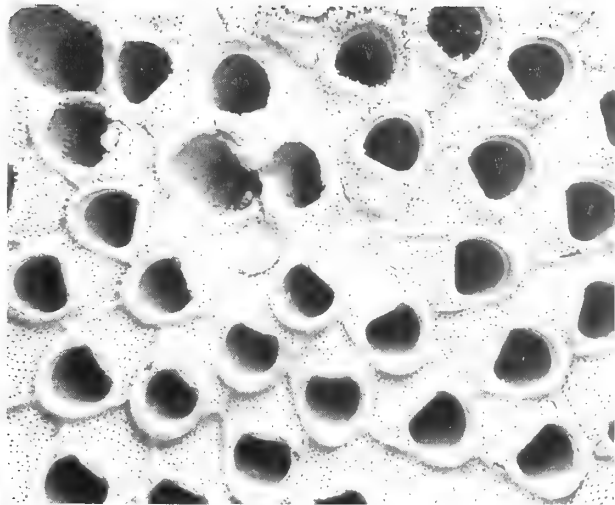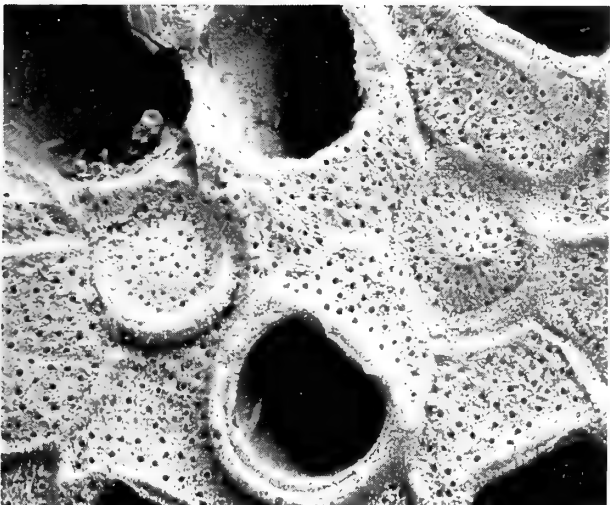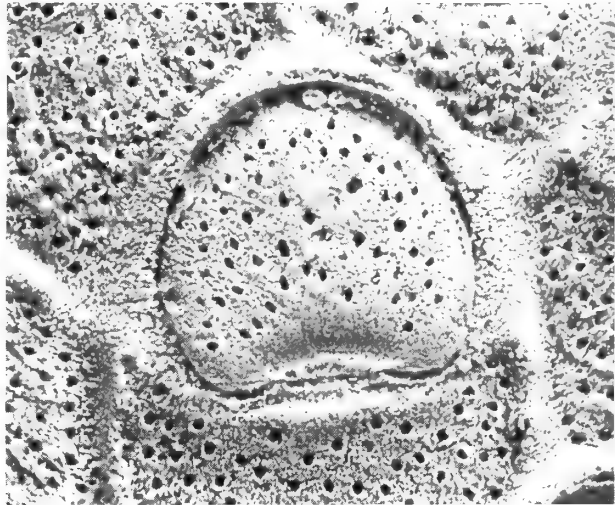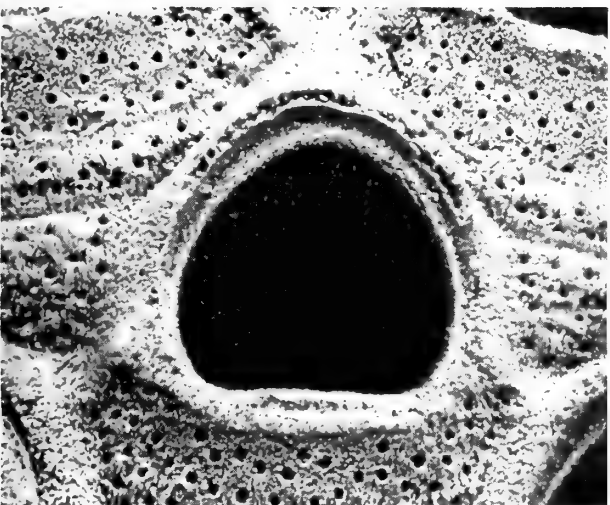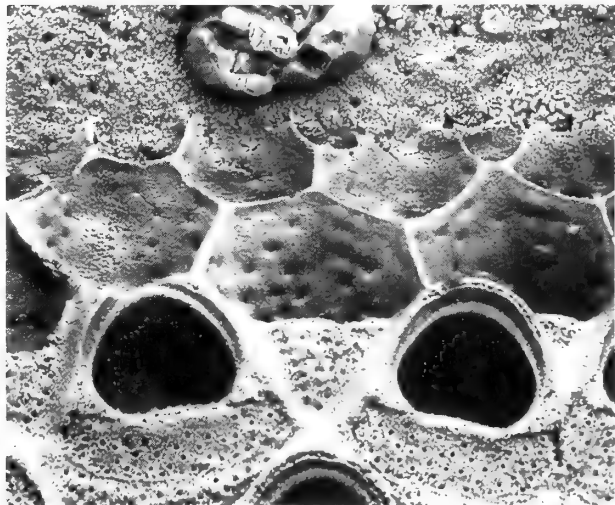
Figs 211–216 *Reptomultelea goldfussi* sp. nov., VH 10426, Lower Cenomanian, Mülheim/Ruhr, Westfalia, Germany; 211, small colony encrusting a shell fragment, × 14; 212, autozooids radiating from two closely-spaced pseudoancestrulae with apertures closed by terminal diaphragms, × 45; 213, detail of occluded pseudoancestrulae, × 130; 214, autozooidal operculum, × 200; 215, autozooidal aperture, × 200; 216, growing edge showing new buds with porous interior walls, × 97.
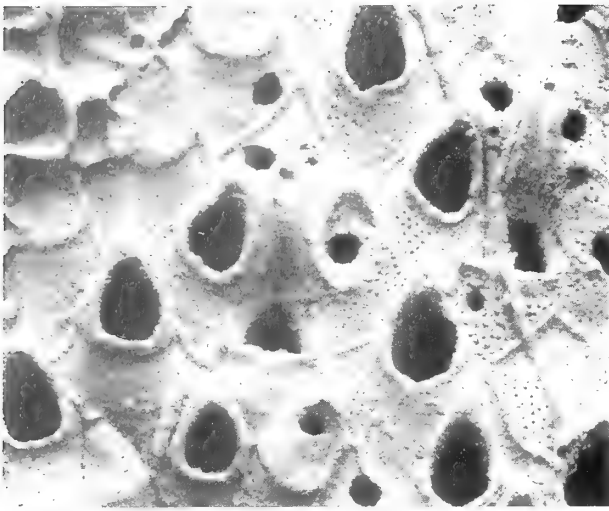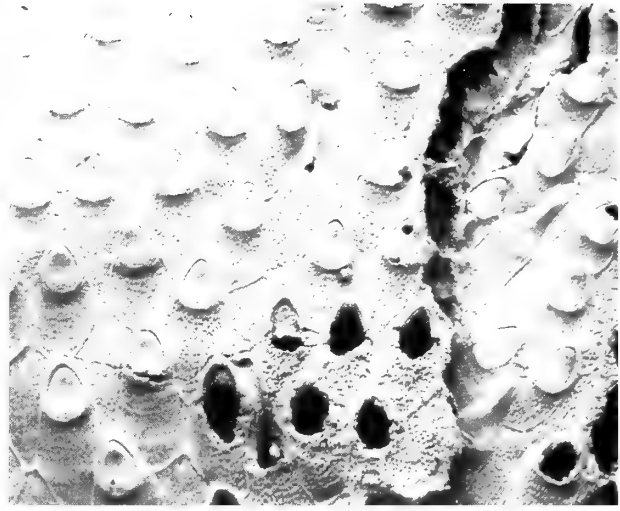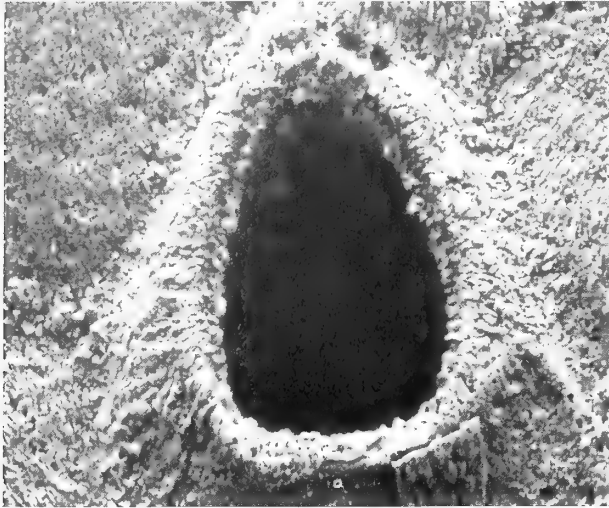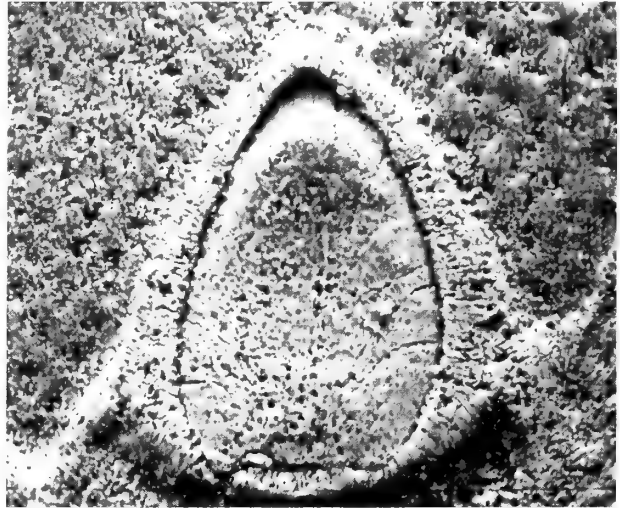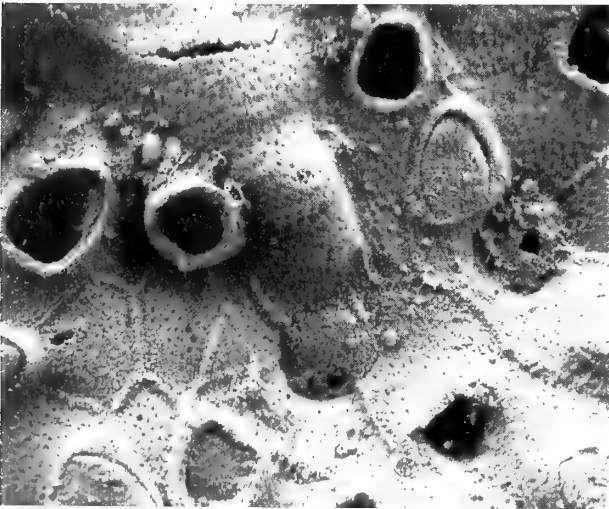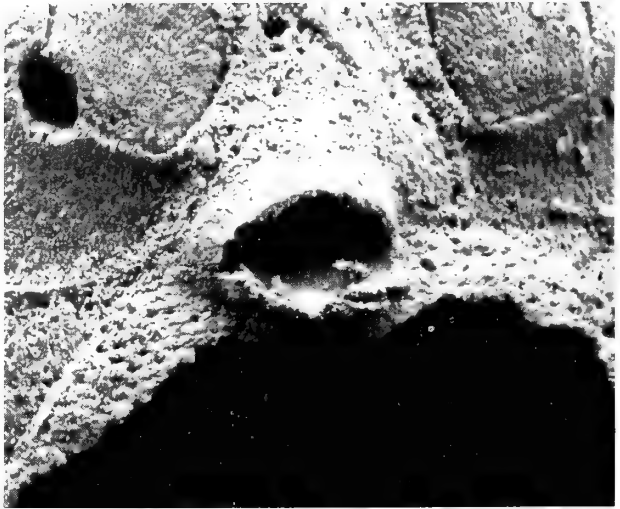
Figs 217–222 *Reptomultelea levinseni* sp. nov. 217, ZMC Levinsen Collection M56, [?Coniacian], Fécamp, Seine Maritime, France; autozooids and two eleozooids with rostra resting on kenozooids, the right-hand eleozooid fouled by a small stomatoporid cyclostome; × 60. 218–222, Coniacian or basal Santonian, *decipiens* Chalk, Vattetot, Seine-Maritime, France. 218–220, BMNH D58930, holotype; 218, partly exfoliated specimen with operculate autozooids and eleozooids, × 28; 219, autozooidal aperture, × 265; 220, autozooidal operculum, × 265. 221, 222, BMNH D59249; 221, gonozooid originating as a first generation bud from a pseudoancestrula (lower centre), × 82; 222, ooeciopore, × 180.

Kenozooids variable in abundance, occasionally isolated but often aggregated, sometimes associated with eleozooids (Fig. 217).

Gonozooids (Fig. 221), known from only one colony (BMNH D52949) which has two, longitudinally elongate, about 1·5 × longer than wide, a short parallel-sided frontal wall emerging from the maternal aperture and dilating to give a subcircular inflated distal frontal wall. Ooeciopore (Fig. 222) transversely elongate. Atrial ring not observed.

MEASUREMENTS.

autozooids (10 zooids with in-situ opercula from holotype BMNH D58930)

frontal length:	mean = 0·66 mm; SD = 0·049 mm; CV = 7·5; range = 0·60–0·75 mm
frontal width:	mean = 0·31 mm; SD = 0·019 mm; CV = 6·2; range = 0·27–0·33 mm
apertural length:	mean = 0·23 mm; SD = 0·008 mm; CV = 3·4; range = 0·23–0·24 mm
apertural width:	mean = 0·16 mm; SD = 0·009 mm; CV = 5·2; range = 0·15–0·18 mm

eleozooids (8 zooids from holotype BMNH D58930)

frontal length:	mean = 1·04 mm; SD = 0·114 mm; CV = 10·9; range = 0·90–1·23 mm
frontal width:	mean = 0·29 mm; SD = 0·014 mm; CV = 4·7; range = 0·27–0·32 mm
apertural length:	mean = 0·52 mm; SD = 0·067 mm; CV = 12·9; range = 0·41–0·60 mm
apertural width:	mean = 0·18 mm; SD = 0·025 mm; CV = 13·6; range = 0·15–0·20 mm

gonozooids (2 zooids from BMNH D52949)

frontal length:	1·70–1·80 mm
frontal width:	1·05–1·20 mm
ooeciopore length:	0·08 mm
ooeciopore width:	0·11 mm

REMARKS. This new Coniacian/Santonian species is very similar to *Reptomultelea sarthacensis* from the Cenomanian-?Lower Turonian (see p. 54). The shape and size of the autozooid and eleozooid apertures are indistinguishable in the two species, but *R. levinseni* has autozooids and eleozooids with longer frontal walls, as reflected in the larger frontal length of these zooids (mean values of 0·66 mm for autozooids and 1·04 mm for eleozooids in *R. levinseni* versus 0·48–0·55 mm for autozooids and 0·70–0·81 mm for eleozooids in *R. sarthacensis*).

A notable feature of the only fertile colony available (BMNH D52949) is the budding of gonozooids from pseudoancestrulae, well within secondary zones of astogenetic change. In general, gonozooids in multilamellar melicerititids occur exclusively in zones of astogenetic repetition.

Colonies of *Reptomultelea levinseni* from the *decipiens* Chalk occur as nodular or tube-shaped colonies, the latter having probably grown loosely around organic substrates. *R. sarissata* and other bryozoans from here may adopt similar growth-forms.

DISTRIBUTION. Coniacian and/or basal Santonian, Seine Maritime, France.

Reptomultelea matutina sp. nov.   Figs 224–229

MATERIAL. Holotype: BMNH D52565 (several fragments, including an SEM stub, from one colony), Lower Albian
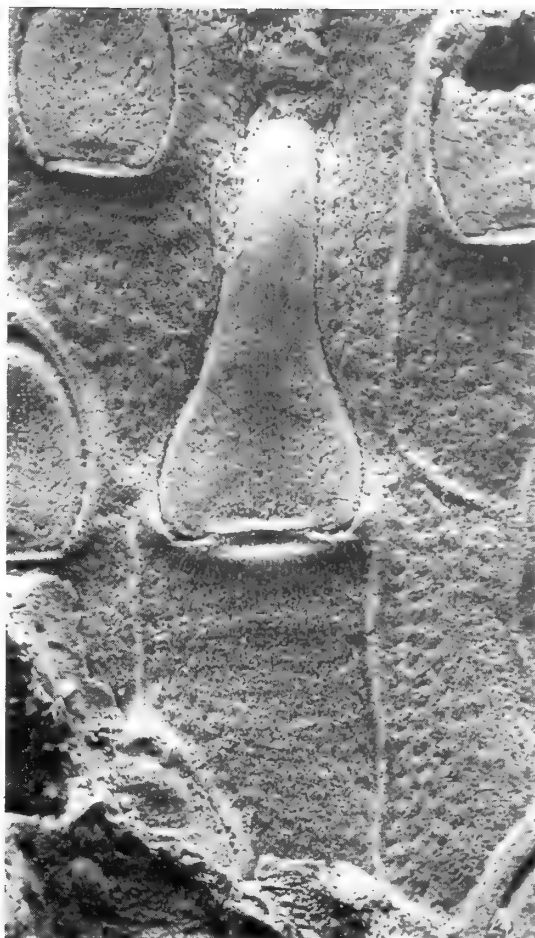
Fig. 223 *Reptomultelea levinseni* sp. nov., BMNH D58930, holotype, Coniacian or basal Santonian, *decipiens* Chalk, Vattetot, Seine-Maritime, France; eleozooid with in-situ operculum, × 160.

(*tardefurcata-mammillatum* Zones), Shenley Limestone, Munday's Hill Pit, Leighton Buzzard, Bedfordshire, England, R.J. Hogg Collection (see Owen 1972).

NAME. From matutinus, Latin for early (in the morning), with reference to the early geological age of the species.

DESCRIPTION. Colony encrusting, multilamellar (Fig. 224), up to 12 or more layers each about 0·20 mm thick. Ancestrula unknown. Overgrowths develop by eruptive budding onto colony surface from closely-spaced autozooidal pseudoancestrulae located in depressions (Fig. 225); apertures of pseudoancestrulae are smaller and less elongate than those of autozooids from zones of astogenetic repetition, being about 0·15 mm long by 0·14 mm wide.

Autozooids (Fig. 226) of large size; frontally elongate, 2–3 × longer than wide, generally rhomboidal, distally extended and well-rounded by aperture; frontal wall occupying most of the frontal area, convex with circular pseudopores set in elongate depressions; zooecial boundary wall prominent. Aperture small, longitudinally elongate, about 1·2–1·3 × longer than wide, attaining maximum width between the hinge line and mid-length, rounded distally; apertural shelf present; apertural rim well-developed; hinge line with

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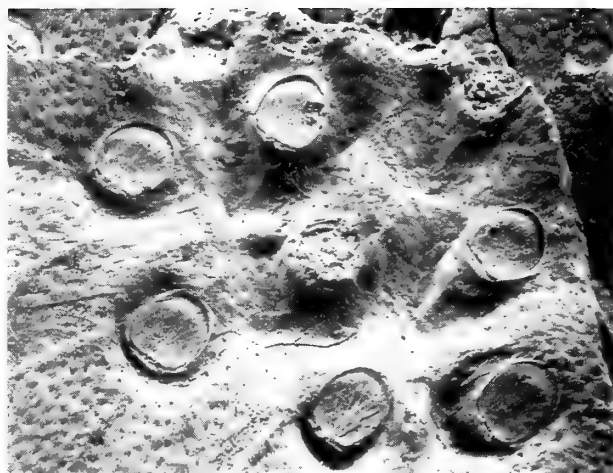
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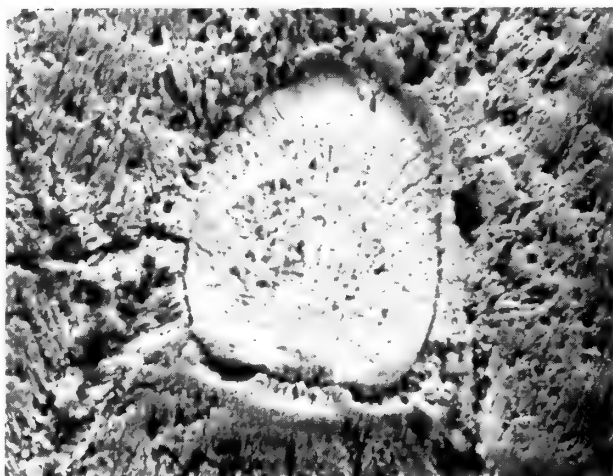
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Figs 224–229 *Reptomultelea matutina* sp. nov., BMNH D52565, holotype, L. Albian *(tardefurcata-mammillatum* Zones), Shenley Limestone, Munday's Hill Pit, Leighton Buzzard, Bedfordshire, England; 224, multilamellar colony with exfoliated layers of autozooids, × 17; 225, depressed area with closely-spaced, operculate pseudoancestrulae, × 60; 226, autozooids growing from top left to bottom right, × 58; 227, autozooidal operculum, × 210; 228, area of coalescent growth, × 41; 229, detail showing kenozooids, × 72.

median bar, raised above general level of frontal surface so that plane of aperture slopes slightly downwards in a distal direction. Operculum (Fig. 227) usually preserved in-situ, surface a little convex, pseudopores apparently absent. Intramural buds and terminal diaphragms not observed.

Eleozooids absent.

Kenozooids (Fig. 229) mainly developed at overgrowth origins and where growing edges from different overgrowths anastomose (Fig. 228), occasionally present elsewhere interspersed among autozooids.

Gonozooids unknown.

MEASUREMENTS.

autozooids (10 zooids with in-situ opercula from holotype BMNH D52565)

frontal length:	mean = 0·72 mm; SD = 0·055 mm; CV = 7·6; range = 0·66–0·81 mm
frontal width:	mean = 0·29 mm; SD = 0·019 mm; CV = 6·7; range = 0·26–0·32 mm
apertural length:	mean = 0·17 mm; SD = 0·009 mm; CV = 5·6; range = 0·15–0·18 mm
apertural width:	mean = 0·13 mm; SD = 0·005 mm; CV = 3·6; range = 0·12–0·14 mm

REMARKS. This is the earliest known species of *Reptomultelea*, and the only species of the genus recorded from the Lower Albian. Only one specimen is known but this is sufficiently different from other species of the genus to warrant recognition as a new species. The absence of eleozooids is best interpreted as a primary characteristic of the species rather than an artefact of small sample size because eleozooids are not developed in areas of anastomosis, where zooid crowding and disruption of the normal budding pattern might be expected to favour their presence. *R. matutina* differs from the somewhat similar *R. oceani* (d'Orbigny) in lacking eleozooids and in having slightly smaller autozooidal apertures.

DISTRIBUTION. Lower Albian of Bedfordshire, England.

Reptomultelea mitrus sp. nov.   Figs 230–234

MATERIAL. Holotype: BMNH D14468, Cenomanian [prob-
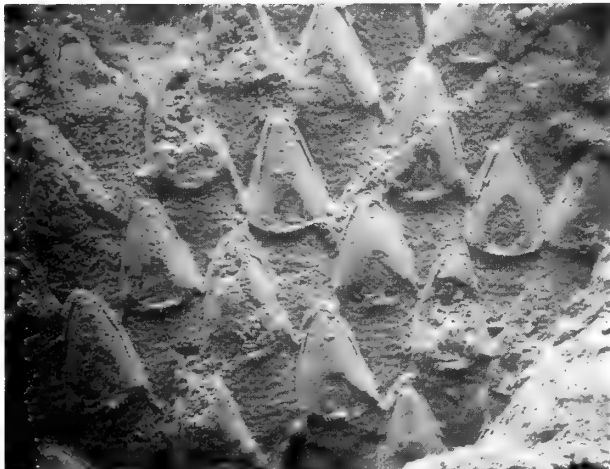
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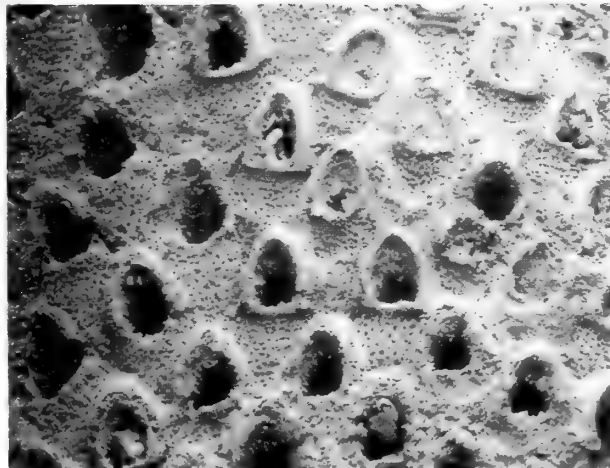
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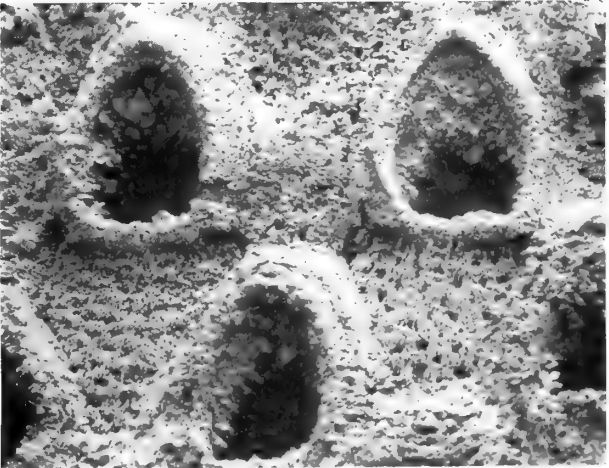
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Figs 230–233 *Reptomultelea mitrus* sp. nov. 230, 231, BMNH D14468, holotype, Cenomanian, Beer Head, Devon, England; 230, operculate autozooids, × 27; 231, detail, × 60. 232, 233, BZ 998, Cenomanian, Wilmington Sands, Grizzle Bed, White Hart Sandpit, Wilmington, Devon; 232, autozooids, × 29; 233, three autozooidal apertures, × 80.

ably Beer Head Limestone Formation, *mantelli* Zone; see Jarvis and Tocher 1987], Beer Head, Devon, England, Bather Collection. Paratype: BZ 998, Cenomanian, Wilmington Sands [a facies of the Beer Head Limestone Fm.], Grizzle Bed, White Hart Sandpit, Wilmington, Devon, Greenaway Colln.

NAME. From Mitra, Latin for head-dress, with reference to the similarity in shape of the operculum to a Bishop's mitre.

DESCRIPTION. Colony multilamellar, each layer about 0·45 mm thick. Ancestrula unknown. Overgrowths arise through intrazooecial fission; pseudoancestrulae are autozooids with apertures about 0·14 × 0·12 mm in size; secondary zones of astogenetic change marked by increasing zooid size and elongation of apertures. Organization fixed-walled. Zooidal apertures closely-spaced, arranged in regular quincunx, disrupted close to overgrowth origins.

Autozooids (Figs 230, 231) of large size, frontally elongate, about 2–3 × longer than wide, typically diamond-shaped in outline but sometimes rhomboidal; frontal wall convex, occupying about half of the frontal surface, with circular pseudopores; boundary wall inconspicuous, slightly salient. Aperture (Fig. 233) very large, elongate, about 1·5 to almost twice as long as wide, attaining maximum width between the hinge line and mid-length, mitre-shaped, pointed distally; apertural rim narrow; apertural shelf narrow, tapering proximally; hinge line with median bar and low teeth at either end. Operculum (Fig. 234) often preserved in-situ, strongly convex; pseudopores elongate, numbering about 20, arranged in an irregular crescent often confined to the proximal half of the operculum. Terminal diaphragms may be present just beneath level of apertural shelf. Intramural buds not observed.

Eleozooids unknown, presumed absent.
Gonozooids not observed.

MEASUREMENTS.
autozooids (10 zooids with in-situ opercula from holotype BMNH D11468)

|	
frontal length:	mean = 0·73 mm; SD = 0·084 mm; CV = 11·4; range = 0·63–0·86 mm
frontal width:	mean = 0·32 mm; SD = 0·022 mm; CV = 7·0; range = 0·30–0·38 mm
apertural length:	mean = 0·35 mm; SD = 0·024 mm; CV = 6·7; range = 0·32–0·38 mm
apertural width:	mean = 0·21 mm; SD = 0·017 mm; CV = 8·1; range = 0·20–0·24 mm

REMARKS. *Reptomultelea mitrus* is characterized by the large and high apertures which are closely-spaced. There is some resemblance with *R. bituberosa* sp. nov., but the prominent tubercles of *R. bituberosa* are totally absent in *R. mitrus* and eleozooids have not been found in this latter species. Apertures in the paratype specimen (Figs 232, 233) of *R. mitrus* are less longitudinally elongate than in the holotype (Figs 230, 231), but this may be due to proximity to overgrowth origins within secondary zones of astogenetic change. Characteristic of the species are the strongly convex opercula and typically diamond-shaped frontal outlines of the zooids. The most prominent, proximal areas of the opercula are often missing in the holotype following exfoliation of overlying layers of the colony (Figs 230, 234).

Neither the holotype nor the paratype preserve their original substrates which may have been aragonitic shells.

The paratype is a 'taco-shaped' colony which apparently grew over the edge of a partly enveloped tabular substratum, possibly a bivalve shell fragment.

DISTRIBUTION. Cenomanian of Devon, England.

Reptomultelea oceani (d'Orbigny, 1850)   Figs 235–242

1850   *Diastopora oceani* d'Orbigny: 176.
1853   *Reptelea oceani* (d'Orbigny); d'Orbigny: 641, pl. 636, figs 5, 6.
non 1872   *Diastopora oceani* (d'Orbigny); Reuss: 110, pl. 27, figs 2, 3.
1890   *Reptelea oceani* (d'Orbigny); Pergens: 399.
1899   *Reptelea pulchella* (d'Orbigny) var. *plana* (d'Orbigny); Gregory: 292 (partim), fig. 31.
non 1899b   *Reptelea oceani* (d'Orbigny); Gregory: 295.
1906   *Semimultelea irregularis* d'Orbigny; Lang: 63.
?1906   *Reptelea oceani* (d'Orbigny); Lang: 63.

MATERIAL. Holotype: MNHN d'Orbigny Collection 6561 (Fig. 235) (Voigt photocards 5681 and 5703), Cenomanian, Le Havre; this specimen measures about 24 × 16 mm and is an excellent match with d'Orbigny's figure (1853: pl. 636, figs

Fig. 234 *Reptomultelea mitrus* sp. nov., BMNH D14468, holotype, Cenomanian, Beer Head, Devon, England, autozooidal operculum, × 205.
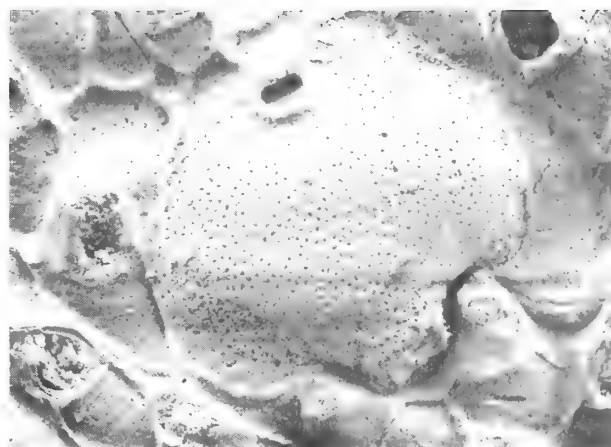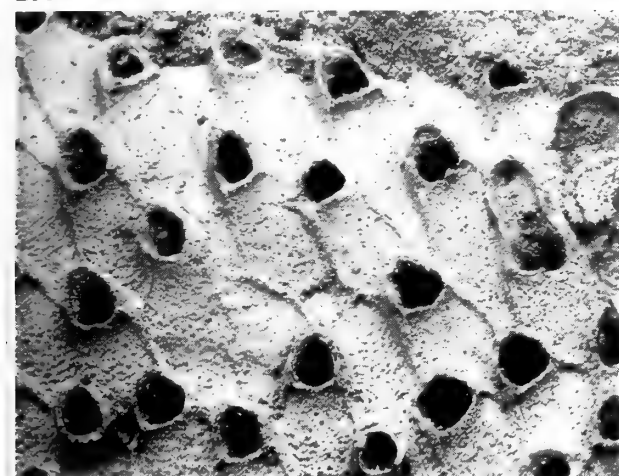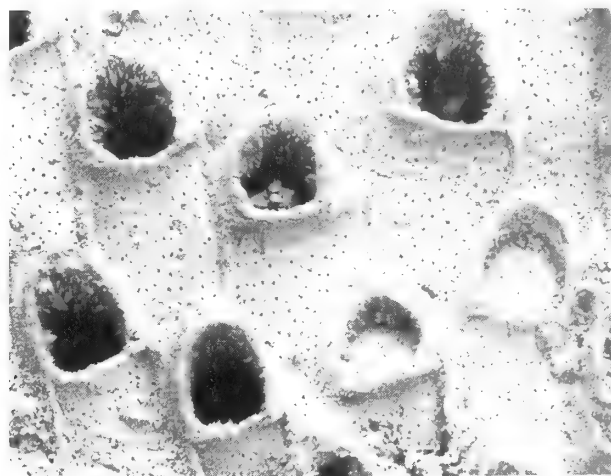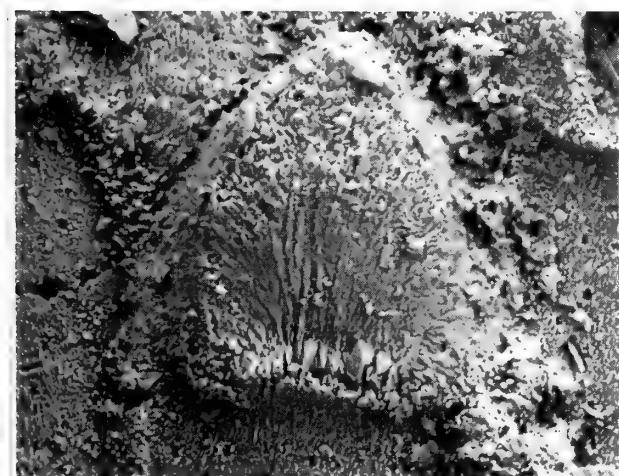
Figs 235–240 *Reptomultelea oceani* (d'Orbigny, 1850). 235, photograph of MNHN d'Orbigny Collection 6561, holotype, Cenomanian, Le Havre, Seine Maritime, France, × 12. 236, BMNH D4387, Cenomanian, Craie chloritée, Cap de la Hève, Seine Maritime, France, gonozooid with associated autozooids and kenozooids, × 50. 237, BMNH D58737, Cenomanian, Cap de la Hève, autozooids, kenozooids and an eleozooid, × 43. 238–240, VH 10447, Cenomanian, Cap de la Hève; 238, autozooids, the two in the lower right closed by terminal diaphragms with central depressions, × 75; 239, autozooidal operculum, × 215; 240, autozooid with broken operculum and terminal diaphragm beneath, × 198.

5, 6), although the image is reversed in the figure.

Other material: VH 10447, Cenomanian, Cap de la Hève, Seine Maritime, France. VH 10446, Lower Cenomanian, *carcitanensis* Zone, Carriére du Billot, Notre-Dame-de-Fresnaye, Calvados, France, G. Breton Colln. BGS GSM 118079, 118081, 118083, 118085–7, 118103, [Lower Cenomanian], Warminster Greensand, Warminster, Wiltshire, England, purchd from W. Cunnington, 1875. BMNH D7274, [Cenomanian, Warminster Greensand, Warminster], mentd by Lang (1906: p. 63). BMNH D57561–6, Cenomanian, Warminster Greensand, Warminster, J.E. Lee Colln presd 1885. BMNH D59205–6, Upper Albian, Upper Greensand, Chert Beds (about 10 m beneath top), Beer Head, Devon, colld by P.D. Taylor, 1985. BMNH D4387, Cenomanian, Craie chloritée, Cap de la Hève, Seine Maritime, France, figd as *Reptelea pulchella* var. *plana* by Gregory (1899, fig. 31). BMNH D55059–61, Cenomanian, Le Havre, Seine Maritime, France, S. Whiteley Colln. BMNH D58737, Cenomanian, Cap de la Hève, Pitt Colln. BMNH D58899, Lower Cenomanian, Craie Glauconieuse, Cap de la Hève, colld by P.D. Taylor & J. Hammond, 1985. BMNH D58924 (4 pieces), Lower Cenomanian, Craie Glauconieuse, Bruneval, Seine Maritime, colld by P.D. Taylor & J. Hammond, 1985.

Questionably assigned: BMNH D55565, Lower Cenomanian, Glauconitic Marl, Rocken End, Isle of Wight, England, C.W. Wright Colln, 1934.

DESCRIPTION. Colony encrusting, multilamellar (Fig. 235), with layers about 0·3 mm thick. Overgrowths develop by eruptive budding onto the surface of the colony; pseudoancestrula usually an autozooid, chamber continuous with the underlying zooid, which undergoes intrazooecial fission to bud pseudoancestrula and encircling zooids of the overgrowth; zone of secondary astogenetic repetition centred on overgrowths is extensive. Ancestrula not observed. Organization fixed-walled. Autozooids commonly arranged in approximate quincunx.

Autozooids (Figs 237, 238) of large size, frontally elongate, on average 2·5 × longer than wide, irregularly rhomboidal or hexagonal in outline shape, rounded to subrounded distally; frontal wall occupying most of the frontal area, slightly convex with circular pseudopores; zooecial boundary wall prominent but thin. Aperture moderately large, longitudinally elongate, 1·1–1·3 × longer than wide, attaining maximum width about mid-length, moderately rounded; apertural rim well-developed, often pointed distally and elevated so that the plane of the aperture slopes upwards in a distal direction; apertural shelf slight; hinge line bowed, apparently with a median bar. Opercula (Fig. 239) quite often found in-situ, convex, pseudopores not observed. Terminal diaphragms (Fig. 238) sometimes present, generally located well proximal to the apertural rim, in one example underlying a broken operculum (Fig. 240), sparsely pseudoporous and with a central depression and pore. Intramural buds not observed.

Eleozooids (Figs 237, 241, 242) moderately abundant, scattered among autozooids in zones of secondary astogenetic change and repetition; frontal surface large, about 3 × longer than wide, appreciably longer and a little wider than autozooids; frontal wall occupying about half of the frontal surface, pseudopore density not differing from that of autozooids. Aperture elongate, 2–2·5 × longer than wide, slightly spatulate or less often parallel-sided, well-rounded distally; rostrum forming an extensive platform. Terminal diaphragms sometimes present (Fig. 241), occupying a variable propor-

tion of the aperture, sparsely pseudoporous. Opercula not observed. Intramurally budded autozooids may be present in eleozooids (Fig. 242).

Kenozooids especially common in zones of secondary astogenetic change close to overgrowth origins, in areas of anastomosis between overgrowths, and associated with gonozooids (Fig. 236).

Gonozooids (Fig. 236) present in a minority of specimens, although more than 10 examples occur in one moderately-sized colony (VH 10446). Frontal wall equidimensional or up to almost twice as long as wide, with a short parallel-sided portion emerging from the maternal aperture, inflated and densely pseudoporous. Atrial ring present. Ooeciopore transversely elliptical, twice as wide as long, a short and reflexed ooeciostome developed in BMNH D4387.

MEASUREMENTS.
autozooids (10 zooids from VH 10447)

frontal length:	mean = 0·70 mm; SD = 0·066 mm; CV = 9·4; range = 0·62–0·83 mm
frontal width:	mean = 0·28 mm; SD = 0·015 mm; CV = 5·3; range = 0·27–0·32 mm
apertural length:	mean = 0·20 mm; SD = 0·018 mm; CV = 8·6; range = 0·18–0·23 mm
apertural width:	mean = 0·17 mm; SD = 0·014 mm; CV = 8·5; range = 0·15–0·20 mm

eleozooids (10 zooids from VH 10447)

frontal length:	mean = 0·96 mm; SD = 0·081 mm; CV = 8·4; range = 0·86–1·16 mm
frontal width:	mean = 0·32 mm; SD = 0·032 mm; CV = 9·8; range = 0·30–0·41 mm
apertural length:	mean = 0·42 mm; SD = 0·026 mm; CV = 6·3; range = 0·36–0·45 mm
apertural width:	mean = 0·18 mm; SD = 0·010 mm; CV = 5·5; range = 0·17–0·20 mm

gonozooids (8 zooids from VH 10446)

frontal length:	mean = 1·56 mm; SD = 0·219 mm; CV = 14·0; range = 1·29–1·80 mm
distal frontal wall length:	mean = 1·30 mm; SD = 0·204 mm; CV = 15·7; range = 1·07–1·53 mm
frontal width:	mean = 0·91 mm; SD = 0·086 mm; CV = 9·4; range = 0·84–1·05 mm
ooeciopore length:	*ca* 0·06 mm
ooeciopore width:	*ca* 0·12 mm

REMARKS. This species is characterized by its eleozooids with rostra well-rounded distally and spatulate or parallel-sided. Among other species of *Reptomultelea* of similar general morphology, *R. oceani* can be most easily distinguished by the spatulate shape of most of the eleozooid apertures.

Reptomultelea oceani is abundant in the Lower Cenomanian Craie Glauconieuse of Normandy and is also common in the approximately contemporaneous Warminster Greensand of Wiltshire. Specimens from the Warminster Greensand tend to have squatter autozooids than those from the Craie Glauconieuse. A specimen from the Glauconitic Marl (BMNH D55565) is assigned to this species with some reservation because of the distinctly narrower eleozooid aperture and slight differences in autozooid morphology.

DISTRIBUTION. Upper Albian-Lower Cenomanian of SW England and Normandy.

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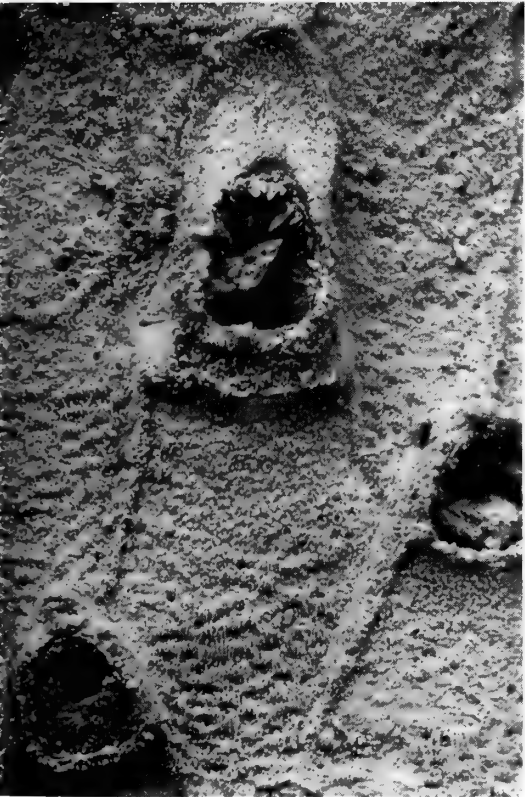
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Figs 241–242 *Reptomultelea oceani* (d'Orbigny, 1850), Cenomanian, Cap de la Hève, Seine Maritime, France. 241, VH 10447, eleozooid with terminal diaphragm, × 115. 242, BMNH D58737, eleozooid containing intramural autozooid, × 112.

Reptomultelea parvula sp. nov. Figs 243–248

MATERIAL. Holotype: VH 10434, Lower Cenomanian, Mülheim/Ruhr, Westfalia, Germany, Klaumann Colln.

NAME. Parvus, small (L.), with reference to the small size of the zooids.

DESCRIPTION. Colony multilamellar with thin layers, each layer about 0·15 mm thick, a transversely folded basal lamina grows free of the bioimmured substratum (?sponge) in the holotype. Ancestrula not observed. Overgrowths (Fig. 243) originate throug.' eruptive budding onto the colony surface (presumably as a result of intrazooecial budding); pseudoancestrula an autozooid with a minute aperture, about 0·09 mm long by 0·06 mm wide, depressed beneath the general level of the colony surface; autozooids in secondary zone of astogenetic change with relatively small, distally rounded apertures; eleozooids in secondary zone of change with short rostra. Organization fixed-walled. Zooids arranged in approximate quincunx.

Autozooids (Figs 245–247) small, frontally elongate, on average slightly over twice as long as wide, typically hexagonal, pointed distally; frontal wall occupying over half of the frontal surface, convex, sparsely pseudoporous; boundary wall well-defined, salient. Aperture (Fig. 248) of small size, on average 1·5 × longer than wide, gothic arch-shaped, attaining maximum width somewhat proximally of mid-length; apertural rim well-developed, prolonged into a tubercle-like structure distally; apertural shelf narrow; hinge bar and teeth not observed. Operculum (Fig. 244) often preserved in-situ, medioproximal surface flat or concave, distolateral edges slightly convex; pseudopores numbering about 16, radially elongate, arranged in a crescent parallel to the distolateral margins. Terminal diaphragms and intramural buds not observed.

Eleozooids (Figs 245–247) very abundant, scattered throughout zones of astogenetic change and repetition; small, frontal surface about 2·5 × longer than wide, similar in width to autozooids but rather longer; frontal wall occupying about half of the frontal surface, sparsely pseudoporous. Aperture elongate, 2–3 × longer than wide, widest close to the hinge line, with a long, narrow rostral area, sometimes very slightly spatulate and rounded distally; apertural rim prolonged into a tubercle-like structure distally. Opercula often preserved in-situ, surface flat proximally, strongly convex in the narrow distal part of the operculum, proximal edge thickened and bowed; pseudopores radially elongate, arranged in a crescent, becoming more widely-spaced distally. Intramural buds not observed.

Gonozooids (Fig. 243) present in the holotype, longitudinally elongate, about twice as long as wide. a variably lengthed parallel-sided portion emerging from the maternal aperture (Fig. 247) and becoming longitudinally ovoidal. Ooeciopore transversely elongate, about twice as wide as long, its proximal edge indented internally by a hemiseptum. Atrial ring not observed.

MEASUREMENTS.
autozooids (10 zooids from holotype VH 10434)

frontal length:	mean = 0·39 mm; SD = 0·033 mm; CV = 8·5; range = 0·35–0·45 mm
frontal width:	mean = 0·18 mm; SD = 0·010 mm; CV = 5·5; range = 0·17–0·20 mm
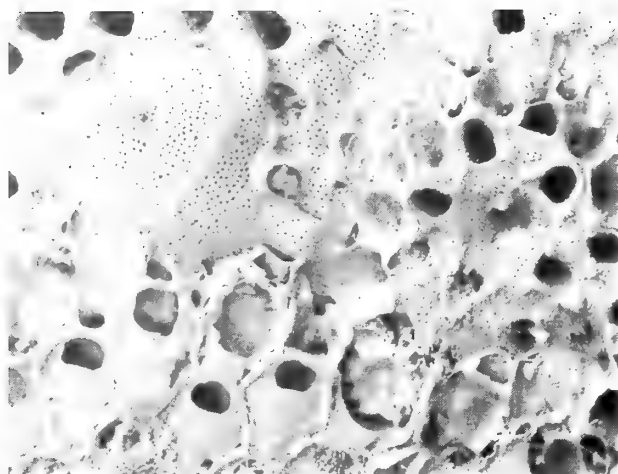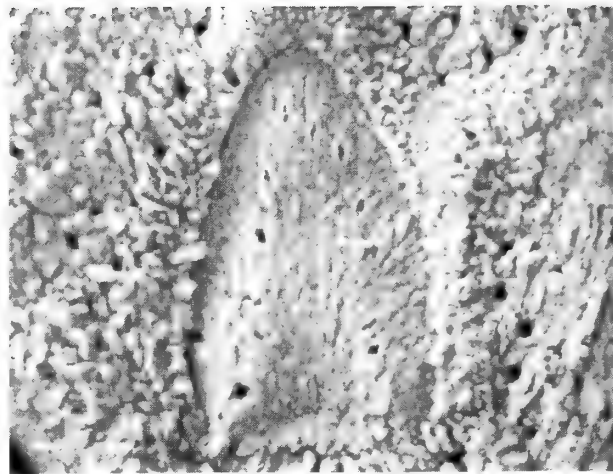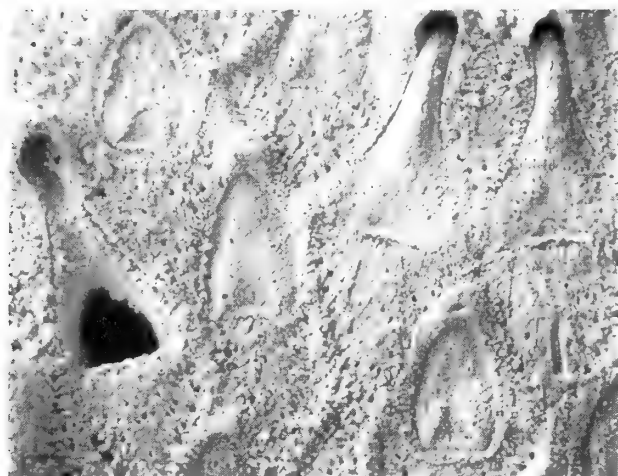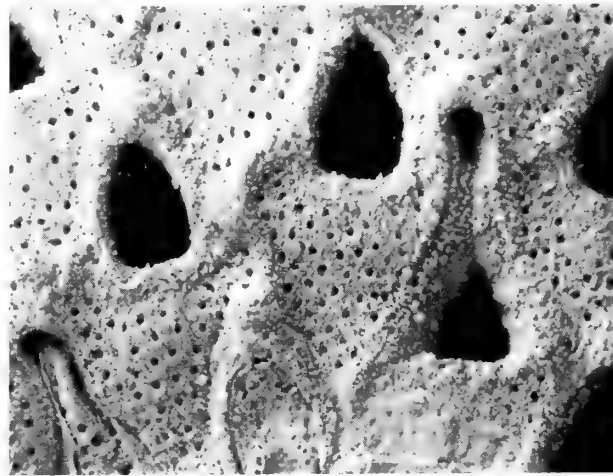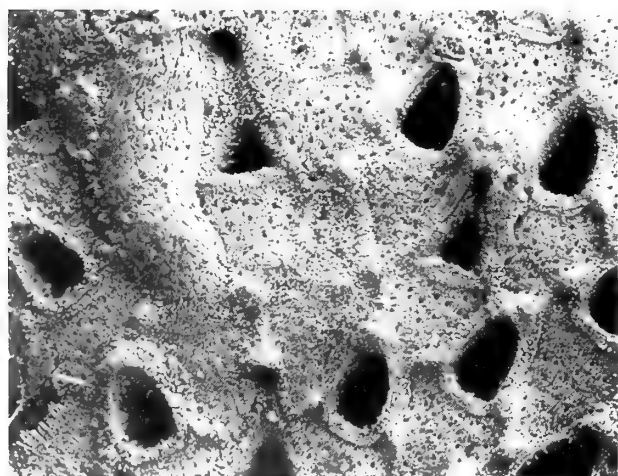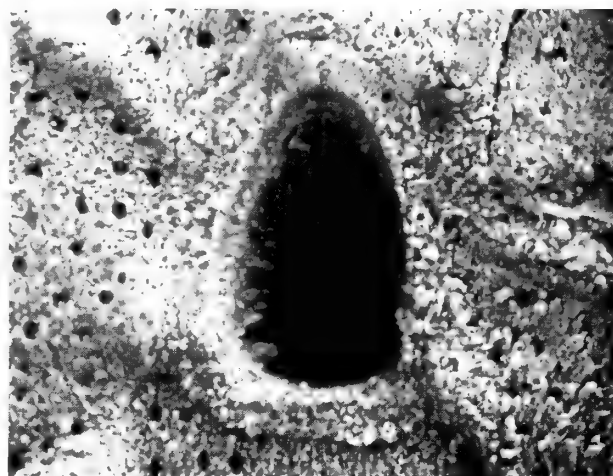
Figs 243–248 *Reptomultelea parvula* sp. nov., VH 10434, holotype, Lower Cenomanian, Mülheim/Ruhr, Westfalia, Germany; 243, gonozooid (left), small intrazoarial overgrowth (right), and an overgrowing onychocellid cheilostome (bottom), × 40; 244, autozooidal operculum, × 300; 245, operculate autozooids and three eleozooids, two with in-situ opercula, × 97; 246, autozooids and an eleozooid, × 130; 247, gonozooid origin (left), autozooids and eleozooids, × 85; 248, autozooidal aperture, × 300.

apertural length: mean = 0·15 mm; SD = 0·010 mm; CV = 6·9; range = 0·14–0·17 mm

apertural width: mean = 0·10 mm; SD = 0·008 mm; CV = 8·2; range = 0·09–0·11 mm

eleozooids (10 zooids from holotype VH 10434)

frontal length: mean = 0·45 mm; SD = 0·022 mm; CV = 4·8; range = 0·42–0·48 mm

frontal width: mean = 0·18 mm; SD = 0·021 mm; CV = 11·5; range = 0·15–0·23 mm

apertural length: mean = 0·24 mm; SD = 0·017 mm; CV = 6·8; range = 0·23–0·27 mm

apertural width: mean = 0·09 mm; SD = 0·012 mm; CV = 12·7; range = 0·08–0·12 mm

gonozooids (3 zooids from holotype VH 10434)

frontal length: 1·34 mm (1 zooid)

distal frontal wall length: 0·93–1·14 mm (2 zooids)

frontal width: 0·60–0·68 mm

ooeciopore length: 0·05–0·06 mm

ooeciopore width: 0·11–0·14 mm

REMARKS. This species resembles *Reptomultelea sarthacensis* (d'Orbigny), with which it co-occurs at Mülheim, but has substantially smaller zooids, a difference considered sufficient to warrant its recognition as a new species. Eleozooids seem to be more abundant in *R. parvula* than *R. sarthacensis*, and are present in secondary zones of astogenetic change close to pseudoancestrulae, while autozooidal opercula have a distinct flattened proximal area beyond which is the crescent of pseudopores.

DISTRIBUTION. Lower Cenomanian of Mülheim/Ruhr, Westfalia, Germany.

Reptomultelea pegma sp. nov.   Figs 249–255

MATERIAL. Holotype: VH 10430, Lower Cenomanian, Mülheim/Ruhr, Westfalia, Germany. Paratypes: VH 10431, 10543–6, same horizon and locality as holotype.

NAME. Pegma, shelf (L.), with reference to the broad apertural shelf.

DESCRIPTION. Colony unilamellar or locally multilamellar, with each layer about 0·38 mm thick, typically taking the form of a unilamellar expansion with a transversely folded basal lamina indicating growth into free space independent of a substratum. Colony base not observed. Overgrowths apparently originate by intrazooecial fission (Fig. 250) from a group of basal autozooids; later stages not seen. Organization fixed-walled. Zooids arranged in approximate quincunx.

Autozooids (Figs 249, 253) of moderate size, frontally elongate, about 1·5–2 × longer than wide, subhexagonal in outline with a well-rounded distal border and concave proximo-lateral borders; frontal wall occupying much less than half of the frontal surface, very convex with circular pseudopores; zooecial boundary wall generally absent. Aperture (Fig. 251) moderately large, a little longer than wide, attaining maximum width about mid-length, considerably narrower at the proximal edge, well-rounded and strongly depressed distally; apertural rim usually absent but sometimes developed (? signifying intramural budding); apertural shelf very broad, attaining a width of about 0·06 mm distally, tapering proximally; hinge line very short, raised, bowed. Operculum (Fig. 254) often preserved in-situ, convex, with about 20 elongate pseudopores arranged in a crescent extending from either end of the hinge line to mid-length or a little beyond. Terminal diaphragms (Fig. 252) present in a few autozooids slightly beneath the level of the apertural shelf, sparsely pseudoporous. Intramurally budded autozooids not observed, unless occasional autozooids with apertural rims are intramural buds.

Eleozooids (Figs 249, 255) common, scattered; large, frontal surface over 2 × longer than wide, widest near the distal part of the aperture, almost twice the length and 1·5 × the width of an autozooid; frontal wall occupying less than a third of the frontal surface, very convex with circular pseudopores. Aperture elongate, almost twice as long as wide, distinctly spatulate, well-rounded distally; rostrum forming an extensive platform strongly depressed distally; apertural rim absent; hinge line raised, broken in all available specimens. Opercula not observed in-situ. Intramural buds not seen.

Kenozooids occasionally present, sometimes associated with eleozooids.

Gonozooids not observed.

MEASUREMENTS.

autozooids (10 zooids with in-situ opercula from holotype VH 10430)

frontal length: mean = 0·48 mm; SD = 0·062 mm; CV = 12·9; range = 0·42–0·63 mm

frontal width: mean = 0·27 mm; SD = 0·015 mm; CV = 5·6; range = 0·24–0·29 mm

apertural length: mean = 0·24 mm; SD = 0·019 mm; CV = 8·1; range = 0·23–0·27 mm

apertural width: mean = 0·23 mm; SD = 0·007 mm; CV = 3·4; range = 0·21–0·24 mm

eleozooids (6 zooids from holotype VH 10430)

frontal length: mean = 0·82 mm; SD = 0·048 mm; CV = 5·9; range = 0·75–0·89 mm

frontal width: mean = 0·37 mm; SD = 0·033 mm; CV = 8·8; range = 0·32–0·41 mm

apertural length: mean = 0·55 mm; SD = 0·039 mm; CV = 7·2; range = 0·51–0·60 mm

apertural width: mean = 0·31 mm; SD = 0·029 mm; CV = 9·5; range = 0·27–0·36 mm

[nb. apertural length is an estimated value because all available eleozooids have broken hinge lines]

REMARKS. This distinctive new species is notable for the broad apertural shelf, sunken aperture, small frontal wall and short hinge line of the autozooids. The apertural shelf in particular enables a clear distinction to be made from all other species of *Reptomultelea*.

DISTRIBUTION. Lower Cenomanian of Mülheim/Ruhr, Westfalia, Germany.

Reptomultelea polytaxis (Voigt, 1924)   Figs 256–262

1924 *Semimultelea polytaxis* Voigt: 166, pl. 4, fig. 11, pl. 5, figs 5, 6.

MATERIAL. The types of this species, originally described from Sudmerberg near Goslar and Gr. Bülten near Peine, Westfalia, were destroyed during World War 2. As the identity of *R. polytaxis* is not in doubt, it would serve no useful purpose to designate a neotype.

Other material: BMNH D31068, D39515–7, D39524, Santonian, Gr. Bülten, Westfalia, Germany, Voigt Colln. VH 10304, 10453, L. Santonian, Gr. Vallstedt, nr Braunschweig,
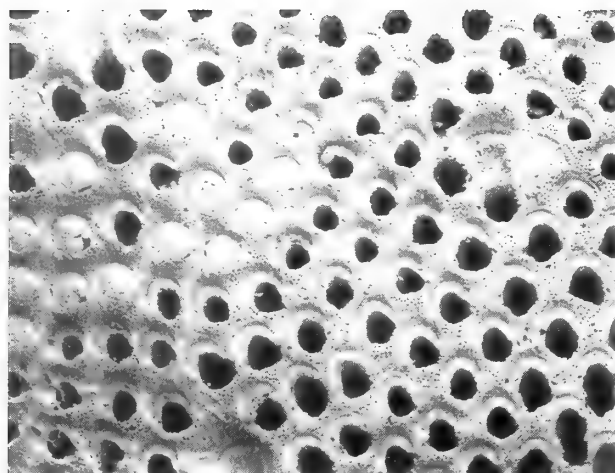
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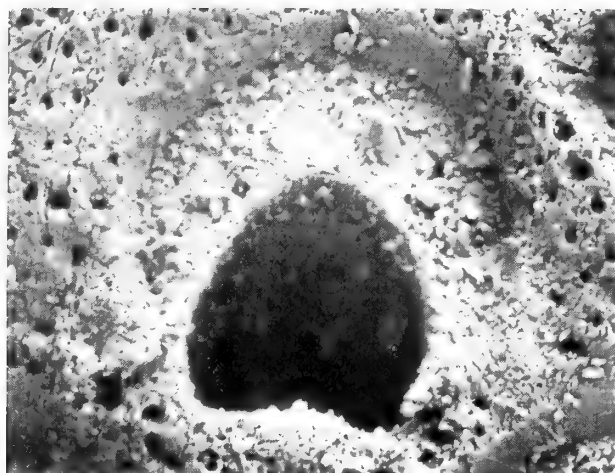
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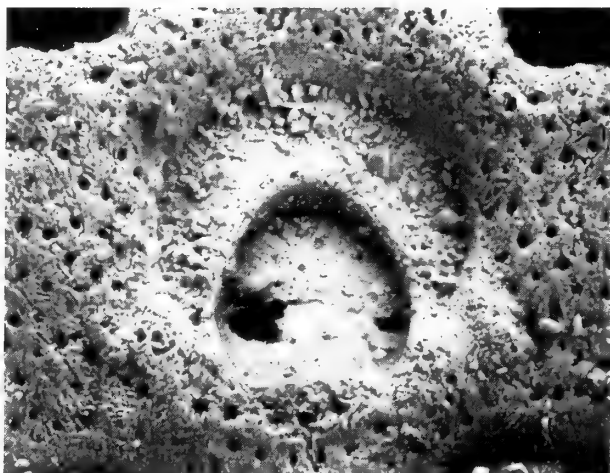
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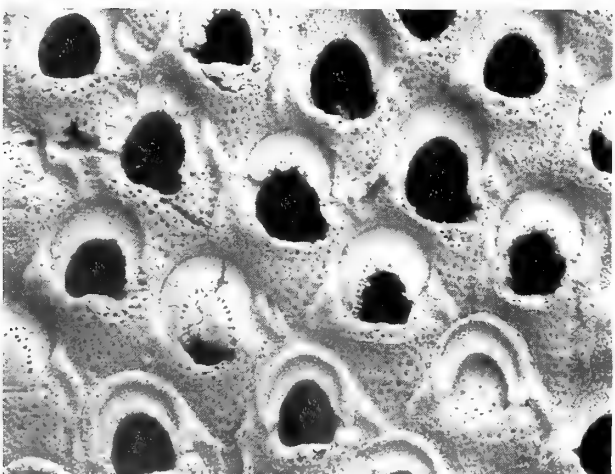
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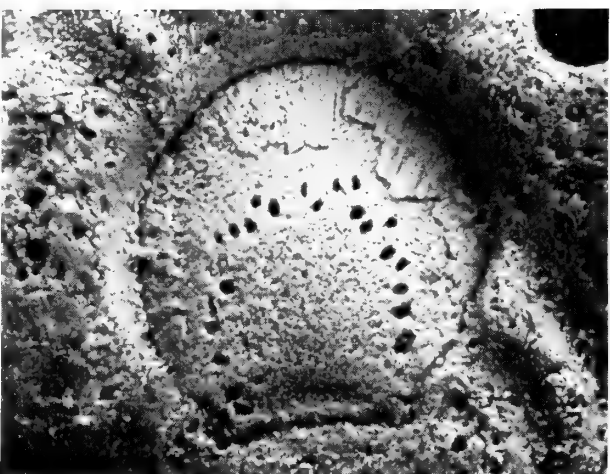
254

Figs 249–254 *Reptomultelea pegma* sp. nov., Lower Cenomanian, Mülheim/Ruhr, Westfalia, Germany. 249–252, VH 10430, holotype; 249, autozooids and eleozooids, × 22; 250, autozooids showing intrazooecial fission, × 55; 251, autozooidal aperture, × 270; 252, autozooidal aperture closed by a terminal diaphragm, × 205. 253, 254, VH 10431; 253, autozooids, × 32; 254, autozooidal operculum, × 270.
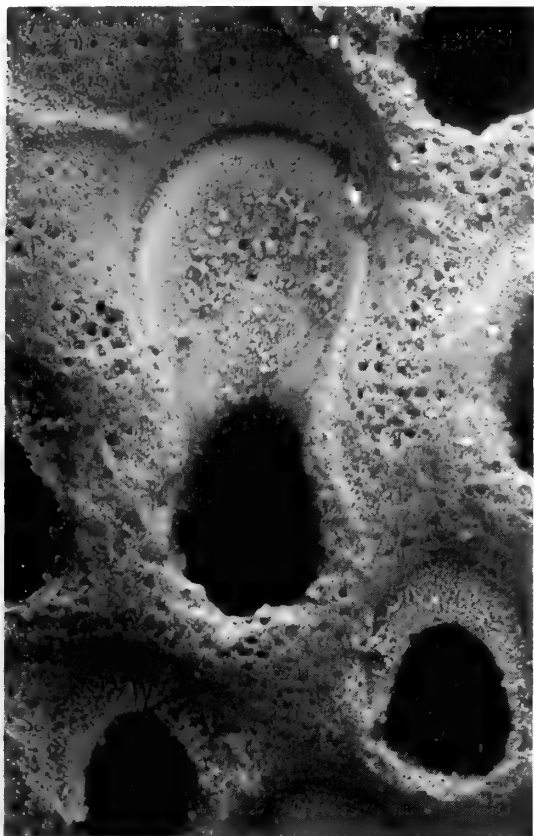
Fig. 255 *Reptomultelea pegma* sp. nov., VH 10430, Lower Cenomanian, Mülheim/Ruhr, Westfalia, Germany; eleozooid with broken hinge line, × 142.

Westfalia, Germany. VH 10440, L. Santonian, Lengede-Broistedt, nr Braunschweig, Westfalia, Germany.

DESCRIPTION. Colony multilamellar, layers variable in thickness from about 0·3–0·5 mm. Basal lamina often growing free of substratum, undulose, when weathered revealing septal trace pattern defining long, narrow basal outlines of zooids (about 0·65 mm long by 0·07 mm wide in VH 10453). Overgrowth origins depressed (Fig. 257), sometimes closely-spaced, originating by intrazooecial fission, the parent zooid forming a central pseudoancestrula surrounded by about 6–7 buds; pseudoancestrula an autozooid or a kenozooid, commencing a secondary zone of astogenetic change of increasing zooid size. Organization fixed-walled. Zooidal apertures irregularly arranged, especially close to overgrowth origins and anastomoses.

Autozooids (Figs 256, 260) small, frontally elongate, about twice as long as wide, usually subhexagonal or subrhomboidal in outline, well-rounded distally; frontal wall almost flat, pseudopores subcircular; boundary wall salient. Aperture (Fig. 259) of small size, longitudinally elongate, on average about 1·25 × longer than wide, attaining maximum width between the hinge line and mid-length, well-rounded distally; apertural rim slightly raised; apertural shelf narrow, tapering proximally; hinge line bowed with a short median ridge between hinge teeth. Operculum (Fig. 258) often preserved

in-situ, convex; pseudopores numbering about 14, circular or a lttle elongated radially, arranged in a crescent. Terminal diaphragms occasionally present (SEM-studied examples poorly-preserved). Intramural buds not observed.

Kenozooids (Figs 256, 260) abundant, scattered among the autozooids and eleozooids mostly in zones of astogenetic repetition away from overgrowth origins.

Eleozooids (Fig. 260) abundant, scattered; small, frontally elongate, generally slightly longer than the autozooids but about the same width, tapering distally. Aperture (Fig. 261) small, longitudinally elongate, trifoliate in outline, on average 1·8 × longer than wide and slightly shorter than the autozooidal apertures; however, eleozooids with larger apertures (0·29 × 0·12 mm) are present in VH 10304; apertural rim moderately raised distally. Operculum not observed in-situ. Intramural buds unknown.

Gonozooids (Fig. 262) represented in only one colony. Longitudinally elliptical in frontal outline, the distal frontal wall commencing with a short parallel-sided tube emerging from the maternal aperture. Ooeciopore transversely elongate, about 1·7 × wider than long. Atrial ring not observed.

MEASUREMENTS.
autozooids (10 zooids with in-situ opercula from VH 10440)

frontal length:	mean = 0·35 mm; SD = 0·045 mm; CV = 12·9; range = 0·29–0·42 mm
frontal width:	mean = 0·17 mm; SD = 0·016 mm; CV = 9·4; range = 0·15–0·20 mm
apertural length:	mean = 0·15 mm; SD = 0·009 mm; CV = 6·2; range = 0·14–0·17 mm
apertural width:	mean = 0·12 mm; SD = 0·005 mm; CV = 3·9; range = 0·12–0·14 mm

eleozooids (10 zooids from VH 10440)

|	
frontal length:	mean = 0·39 mm; SD = 0·042 mm; CV = 10·8; range = 0·33–0·48 mm
frontal width:	mean = 0·18 mm; SD = 0·017 mm; CV = 9·6; range = 0·15–0·21 mm
apertural length:	mean = 0·14 mm; SD = 0·007 mm; CV = 5·2; range = 0·14–0·15 mm
apertural width:	mean = 0·08 mm; SD = 0·011 mm; CV = 14·4; range = 0·06–0·09 mm

gonozooids (2 zooids from VH 10304)

frontal length:	1·80–1·83 mm
distal frontal wall length:	1·52–1·61 mm
frontal width:	1·04–1·28 mm
ooeciopore length:	0·08–0·09 mm
ooeciopore width:	0·11–0·12 mm

REMARKS. *Reptomultelea polytaxis* can be distinguished from the co-occurring *R. canui* (Voigt) by the smaller size of the autozooidal apertures, the trifoliate eleozooidal apertures, and greater proportion of kenozooids. Among species of *Reptomultelea* with trifoliozooids, *R. polytaxis* differs from *R. tuberculata* (d'Orbigny) in its less elongate autozooidal apertures, and from *R. betusora* nom. nov. in the shorter frontal length of the autozooids, longer eleozooidal apertures, and larger gonozooids. Together with *R. parvula* sp. nov. (p. 82), this has the smallest zooids among species of *Reptomultelea*.

Colonies of *R. polytaxis* may attain large size; VH 10304 has about 14 layers of zooids and measures 78 × 30 mm. This particular colony is rather unusual in having relatively few
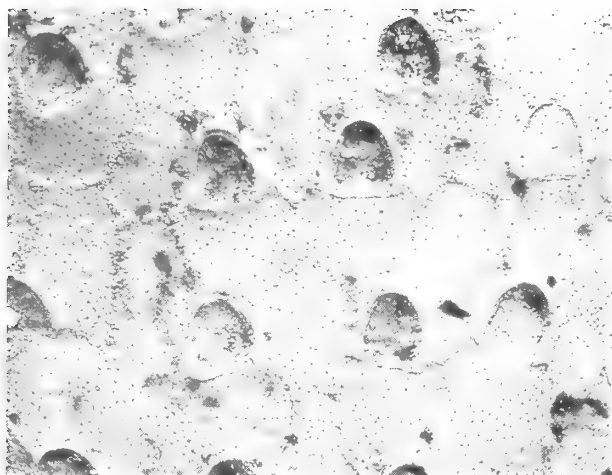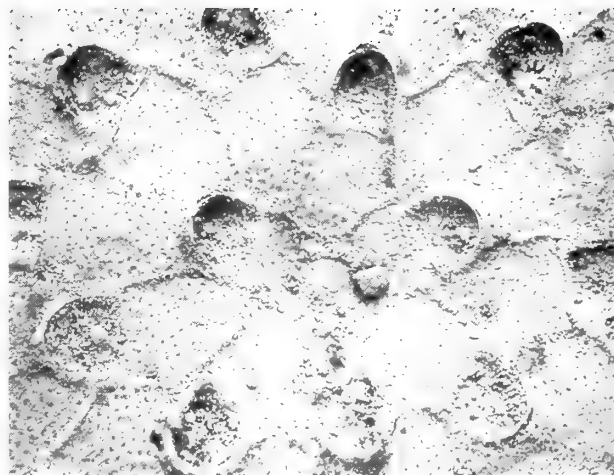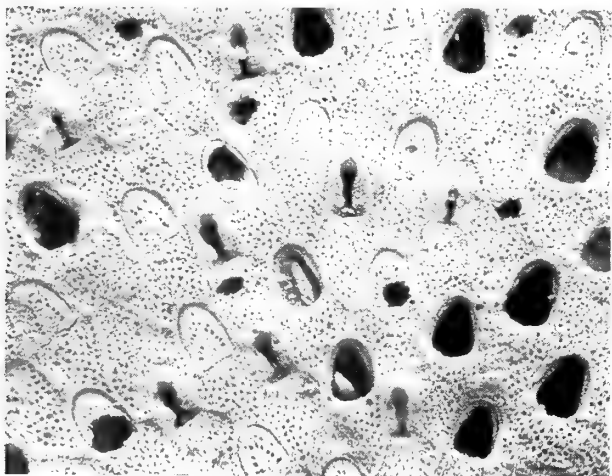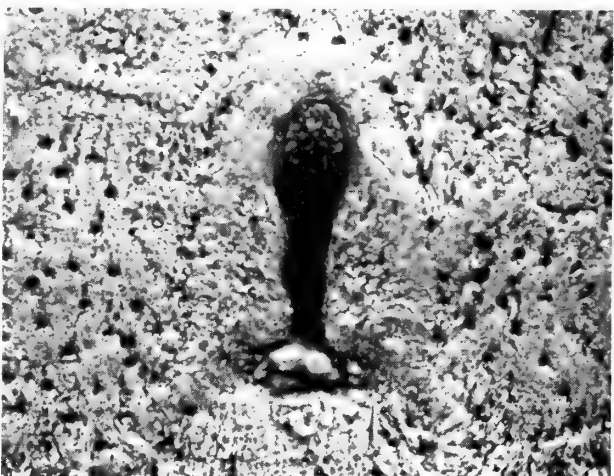
Figs 256–261 *Reptomultelea polytaxis* (Voigt, 1924). 256–259, VH 10304, L. Santonian, Gr. Vallstedt, nr Braunschweig, Westfalia, Germany; 256, autozooids and kenozooids, × 75; 257, overgrowth origin, × 90; 258, autozooidal operculum, × 300; 259, autozooidal aperture, × 300. 260, 261, VH 10440, L. Santonian, Lengede-Broistedt, nr Braunschweig; 260, autozooids, eleozooids and kenozooids, × 55; 261, eleozooidal aperture, × 300.

Fig. 262 *Reptomultelea polytaxis* (Voigt, 1924) , VH 10304, L. Santonian, Gr. Vallstedt, nr Braunschweig, Westfalia, Germany; gonozooid, × 70.

eleozooids which have longer apertures than is typical for the species.

DISTRIBUTION. Santonian of Westfalia, Germany.

Reptomultelea pseudopalpebrosa sp. nov. Figs 263–268

MATERIAL. Holotype: VH 7057, Lower Cenomanian, Mülheim/Ruhr, Westfalia, Germany, Franke Colln.

NAME. With reference to the similarity of the eleozooids to those of *Meliceritites palpebrosa* Levinsen, 1912.

DESCRIPTION. Colony multilamellar, each layer about 0·4 mm thick. Ancestrula not observed. Overgrowths originate by intrazooecial fission, often from a group of adjacent zooids; pseudoancestrula an autozooid, initiating a zone of secondary astogenetic change of increasing zooid size. Organization fixed-walled. Zooid apertures arranged in approximate quincunx. Frontal walls marked by narrow, slightly sinuous, longitudinal stripes of paler and darker hue.

Autozooids (Figs 263–264) of moderate size, frontally elongate, almost twice as long as wide, often rhomboidal in outline, well-rounded distally; frontal wall occupying more than half of the frontal surface, slightly convex and with circular pseudopores; boundary wall discontinuous, absent along some boundaries but raised into flanges or tubercles

elsewhere, especially near the proximo-lateral corners of apertures. Aperture (Fig. 266) moderately large, on average 1·2 × longer than wide, well-rounded distally, attaining maximum width about mid-length; apertural rim absent except in intramural autozooids; apertural shelf broad distally (0·03–0·04 mm), tapering proximally; hinge line with teeth at either end of a median bar. Operculum (Fig. 265) often preserved in-situ, surface convex; pseudopores elongate, arranged in an irregular crescent; sclerites deep (visible as moulds in sediment filling zooecial chambers). Terminal diaphragms present. Intramural autozooids common, differing from primary autozooids in having apertural rims.

Eleozooids common (Figs 263–264), distributed singly or in groups, apparently all intramurally budded and therefore with the same frontal dimensions as autozooids. Apertural area comprises a flat proximal area with few or no pseudopores, a small, D-shaped aperture broader than long and set in an inclined plane directed proximally, and an extensive hood-like distal area (Fig. 268) which is conspicuously pseudoporous, slightly inflated and overlaps the margins of the host aperture. Opercula sometimes in-situ (Fig. 267).

Kenozooids (Figs 263–264) present.

Gonozooids known from a single example, the proximal part of which is obscured. Distal frontal wall subtriangular in outline, broader than long. Ooeciopore transversely elongate, width more than twice the length. Atrial ring not observed.

MEASUREMENTS.
autozooids (10 zooids with in-situ opercula from holotype VH 7057)

|	
frontal length:	mean = 0·49 mm; SD = 0·040 mm; CV = 8·1; range = 0·42–0·54 mm
frontal width:	mean = 0·26 mm; SD = 0·020 mm; CV = 7·8; range = 0·23–0·29 mm
apertural length:	mean = 0·21 mm; SD = 0·013 mm; CV = 6·3; range = 0·20–0·23 mm
apertural width:	mean = 0·17 mm; SD = 0·008 mm; CV = 4·5; range = 0·17–0·18 mm

eleozooids (intramural)

apertural length:	*ca* 0·04–0·05 mm
apertural width:	*ca* 0·07 mm

gonozooids (1 zooid from holotype VH 7057)
distal frontal wall

length:	1·20 mm
frontal width:	1·56 mm
ooeciopore length:	0·09 mm
ooeciopore width:	0·23 mm

REMARKS. Although known from only a single specimen, a variably-preserved colony 37 × 24 mm in size with at least 17 layers of zooids, this species is sufficiently distinctive to warrant formal naming. No other species of *Reptomultelea* has eleozooids with small semicircular apertures and distal, hood-like areas of pseudoporous calcification. In this aspect, *R. pseudopalpebrosa* most closely resembles *Meliceritites palpebrosa* Levinsen, 1912, a vinculariiform species from the Senonian of France. The apertural shelf is similarly broad in the two species, but the abundant pseudopores distributed over the entire surface of the autozooidal opercula in *M. palpebrosa* differ from those of *R. pseudopalpebrosa*, which are arranged in an irregular crescent. A closer affinity seems
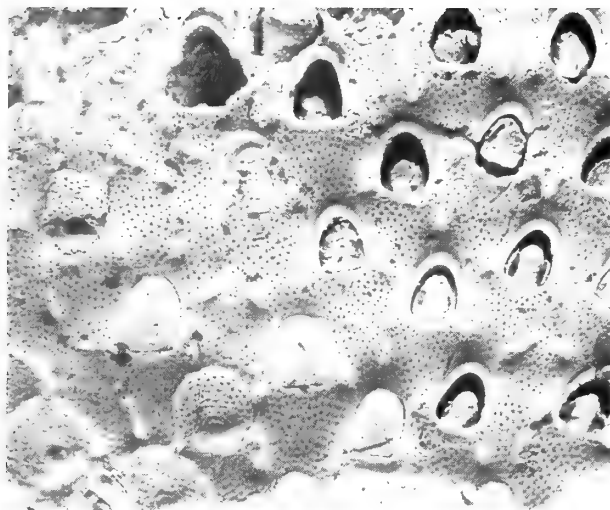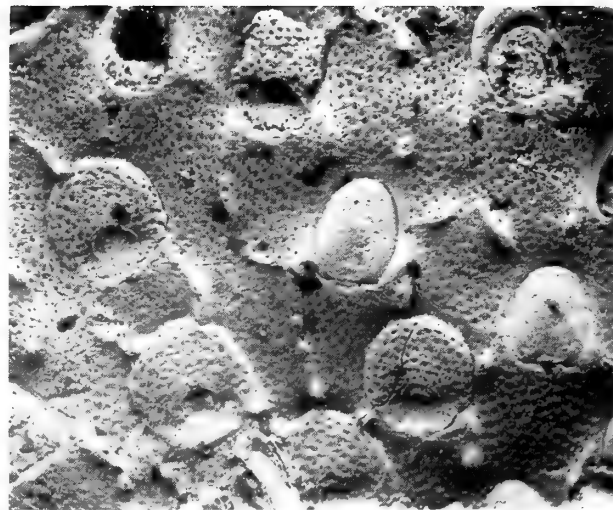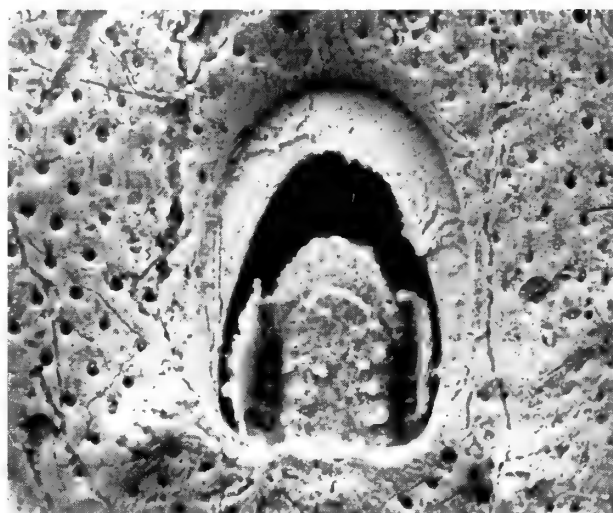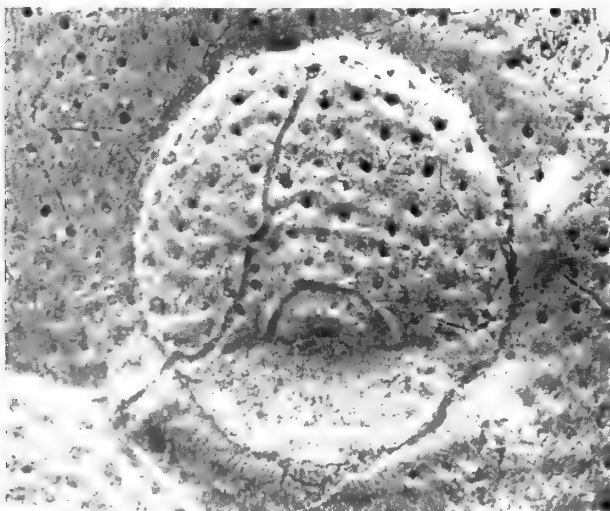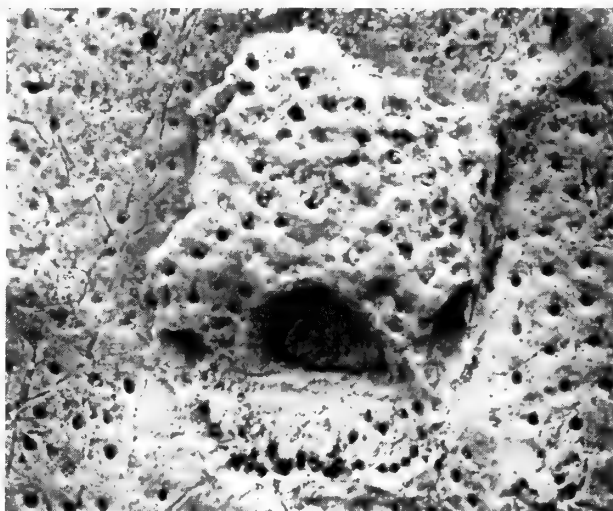
Figs 263–268 *Reptomultelea pseudopalpebrosa* sp. nov., VH 7057, holotype, Lower Cenomanian, Mülheim/Ruhr, Westfalia, Germany; 263, autozooids, eleozooids and kenozooids, × 45; 264, operculate autozooids, kenozooids and eleozooids, × 70; 265, autozooidal operculum, × 265; 266, autozooidal aperture partly occupied by sediment mould of the opercular sclerites, × 265; 267, eleozooid with in-situ operculum, × 265; 268, eleozooid aperture and irregular distal hood, × 265.

possible between the two species than is implied by their inclusion in separate genera. The discontinuous, broken zooecial boundary wall visible on the colony surface of *R. pseudopalpebrosa* is another noteworthy feature, as is the occurrence of slightly sinuous longitudinal stripes of alternating lighter and darker calcification on the frontal walls. The origin and significance of these stripes are unknown.

DISTRIBUTION. Lower Cenomanian of Mülheim, Westfalia, Germany.

Reptomultelea reedi sp. nov. Figs 269–274

MATERIAL. Holotype: VH 10429, Upper Cenomanian, St Calais, Sarthe, France.

NAME. In memory of Christopher G. Reed, whose premature death in 1990 curtailed his elegant studies of bryozoan larval morphology and development.

DESCRIPTION. Colony unilamellar, potentially multilamellar (as indicated by presence of incipient intrazooecial budding), layer thickness about 0·45 mm; basal lamina with closely-spaced transverse ridges and grooves. Ancestrula not observed. Intrazooecial fission present, 5 or 6 daughter buds surrounding the chamber of the parental zooid (Figs 271–272). Organization fixed-walled. Zooid apertures arranged in regular quincunx.

Autozooids (Figs 269, 270) of moderate size, frontally elongate, 1·8–2·4 × longer than wide, outline well-rounded distally but indented proximally by apertures of adjacent zooids; frontal wall convex, occupying more than half of the frontal surface, with circular pseudopores; boundary wall subdued salient. Aperture (Fig. 274) small to medium-sized, equidimensional or a little longer than wide, well-rounded distally, attaining maximum width between hinge line and mid-length; apertural rim present, distally most prominent; apertural shelf widest distally (*ca* 0·02 mm), tapering proximally; hinge-line bowed. Operculum (Fig. 273) often preserved in-situ, surface relatively flat with about 16–18 elongate pseudopores arranged in a crescent parallel to the disto-lateral edges. Terminal diaphragms (Fig. 271) may be developed at a level beneath the apertural shelf. Intramural autozooids may have opercula substantially smaller than primary autozooids, closing beneath the level of the apertural shelf.

Eleozooids observed only as intramural buds within autozooids. Apertures small, longitudinally elongate, almost 1·5 × longer than wide, prominent, set in an oblique plane and directed proximally. Opercula observed in-situ.

Kenozooids rare.

Gonozooids unknown.

MEASUREMENTS.

autozooids (10 zooids with in-situ opercula from holotype VH 10429)

frontal length:	mean = 0·55 mm; SD = 0·059 mm; CV = 10·8; range = 0·47–0·63 mm
frontal width:	mean = 0·26 mm; SD = 0·010 mm; CV = 3·9; range = 0·24–0·27 mm
apertural length:	mean = 0·18 mm; SD = 0·005 mm; CV = 2·6; range = 0·18–0·20 mm
apertural width:	mean = 0·17 mm; SD = 0·007 mm; CV = 4·3; range = 0·17–0·18 mm

eleozooids (intramural)

apertural length:	*ca* 0·15 mm
apertural width:	*ca* 0·11 mm

REMARKS. Only a single specimen of this species is known, a free, unilamellar fragment measuring 8 × 5 mm. The presence of incipient intramural buds indicates that multilamellar growth was possible. *Reptomultelea reedi* most closely resembles the Lower Cenomanian Westfalian species *R. goldfussi* sp. nov. (see p. 73), especially in the well-rounded autozooidal apertures which indent distal zooids, but *R. reedi* has smaller zooids and opercula with pseudopores arranged in a crescent and not all over the surface as in *R. goldfussi*. A further difference between the two species is the presence of intramural eleozooids in *R. reedi*. Well-preserved eleozooidal apertures have not been studied, but the general shape of the opercula suggests that the eleozooids might be of the trifoliozooid-type.

Numerous small borings, probably circular but usually enlarged by chipping of the edges, penetrate the upper surface of this specimen (Fig. 269). Most occur in autozooidal opercula, but some are in terminal diaphragms or frontal walls. They resemble inferred predator borings described from other melicerititid species (Taylor, 1982).

DISTRIBUTION. Upper Cenomanian of Sarthe, France.

Reptomultelea reussi (Pergens, 1890) Figs 275–280

1872   *Diastopora oceani* d'Orbigny; Reuss: 110 (partim), pl. 27, fig. 3 [non fig. 2 = *Reptomultelea sarthacensis* (d'Orbigny)].
1890   *Semielea reussi* Pergens: 399.
?1892   *Semielea reussi* Pergens; Pergens: 278, pl. 11, fig. 7.
1899   *Reptomultelea? reussi* (Pergens); Gregory: 323.
1906   *Reptomultelea reussi* (Pergens); Lang: 63, fig. 10.

MATERIAL. Lectotype (selected herein): SMD un-numbered, the specimen figured by Reuss (1872: pl. 27, fig. 3) (Voigt photocard 2166), Cenomanian [*plenus* Zone], Dresden-Plauen, Germany.

Other material: BMNH D36115, Cenomanian, Untere Planer, Plauen, Dresden, Germany, Pergens Collection. VH 10428, 10433, Cenomanian, *plenus* Zone, Hoher Stein, Dresden-Plauen, Germany.

DESCRIPTION. Colony unilamellar or multilamellar (Fig. 277), each layer about 0·3 mm thick, sometimes cavariiform (Fig. 280) or with layers growing freely of the substratum. Ancestrula, overgrowth origins and pseudoancestrulae not observed. Organization fixed-walled. Zooidal aperture arrangement variable, often rather irregular.

Autozooids (Figs 275, 276) of medium size, frontally elongate, about twice as long as wide, hexagonal, pentagonal or diamond-shaped in outline with a pointed distal end; frontal wall occupying more than half of the frontal surface, slightly convex, with circular pseudopores; boundary wall salient, sometimes poorly developed. Aperture (Fig. 279) of moderate size, about 1·2–1·3 × longer than wide, gothic arch-shaped, pointed distally, attaining maximum width between hinge line and mid-length; apertural rim raised, more prominent distally; apertural shelf absent; hinge line gently bowed, teeth and bar not observed. Operculum rarely preserved in-situ, surface flat; pseudopores arranged in a crescent. Intramurally budded eleozooids may occur. Diaphragms not seen.

Kenozooids possibly present.
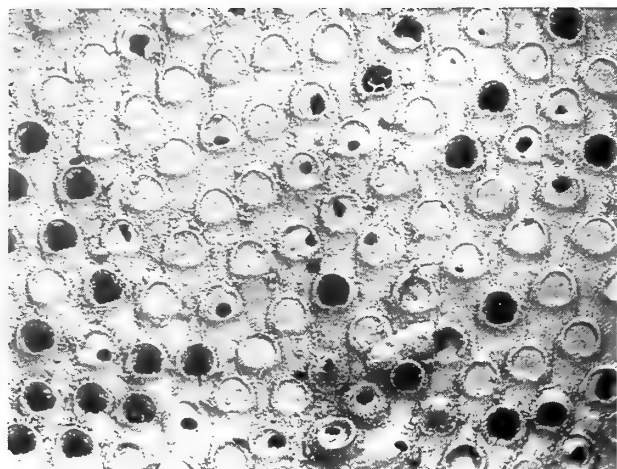
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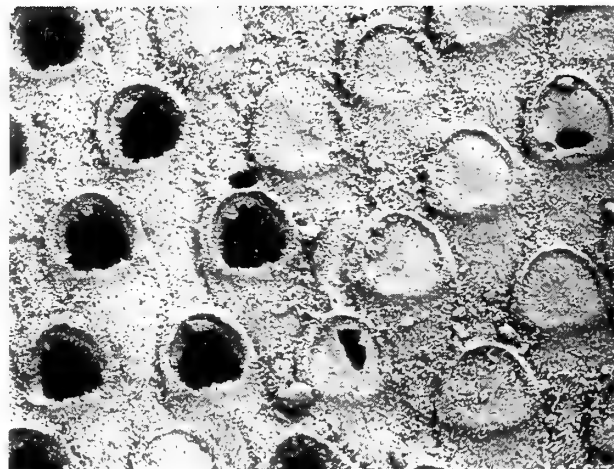
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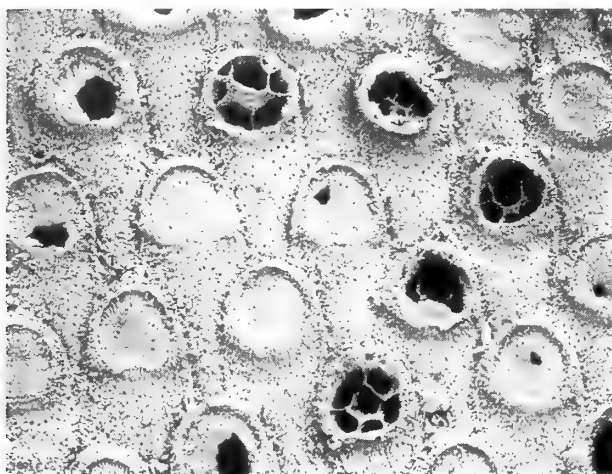
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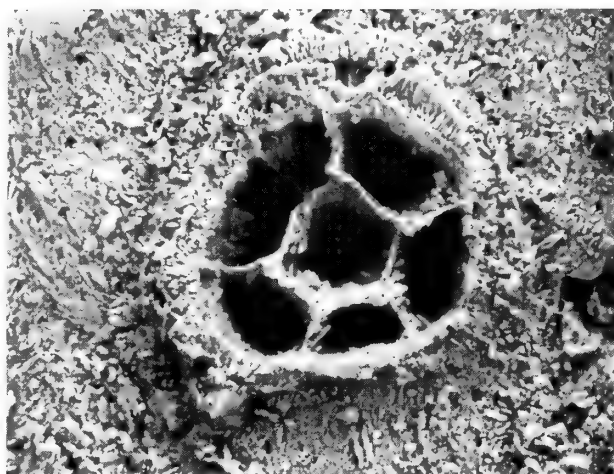
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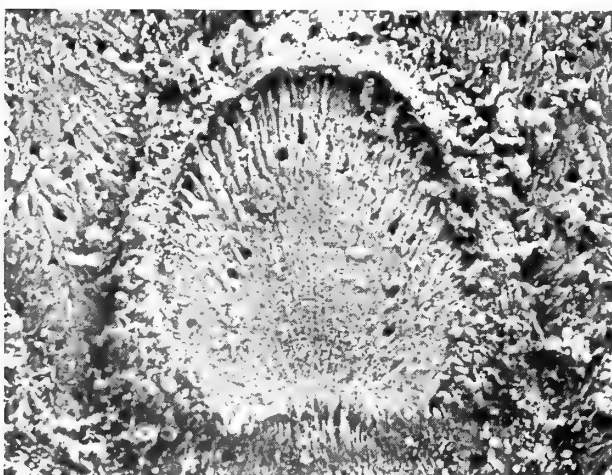
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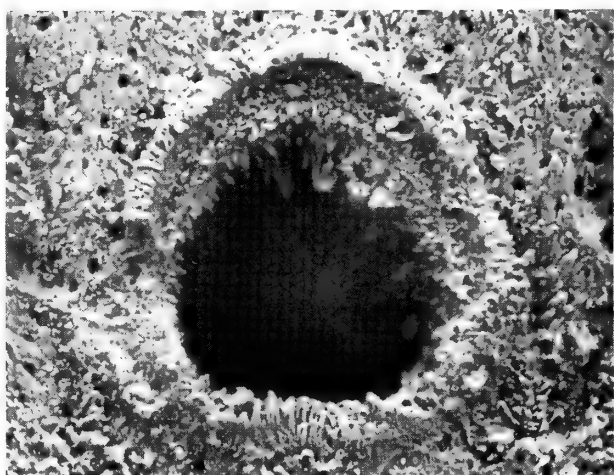
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Figs 269–274   *Reptomultelea reedi* sp. nov., VH 10429, holotype, Upper Cenomanian, St Calais, Sarthe, France; 269, autozooids, some with bored opercula, × 22; 270, operculate and non-operculate autozooids, × 55; 271, autozooids variously with opercula, intrazooecial fissions and a terminal diaphragm (top left), × 55; 272, autozooidal aperture with intrazooecial fission, × 225; 273, autozooidal operculum, × 265; 274, autozooidal aperture, × 265.
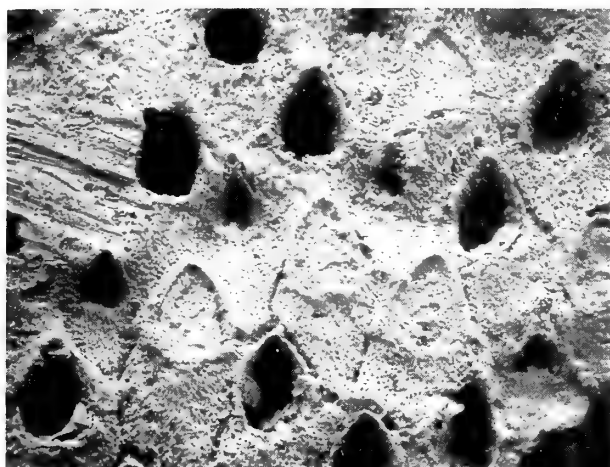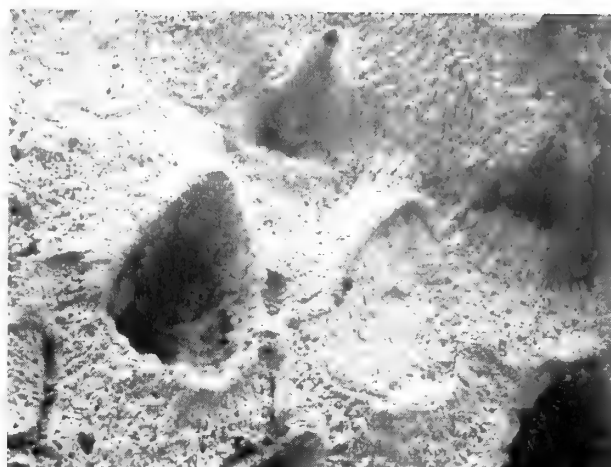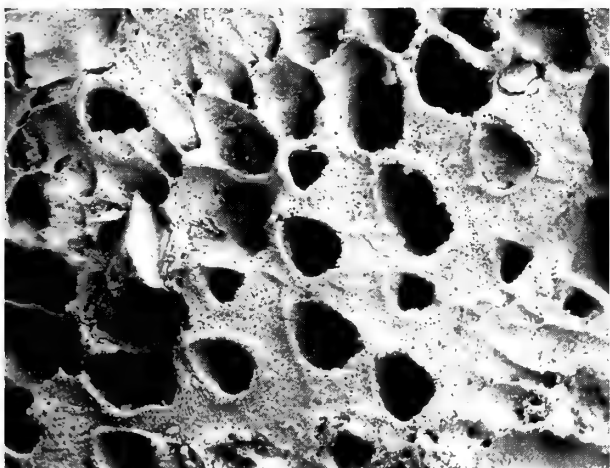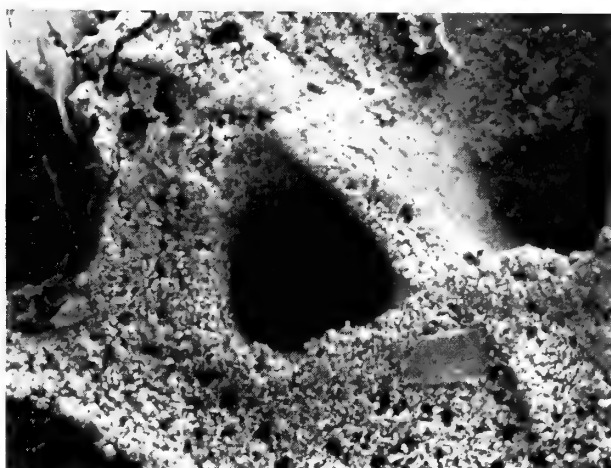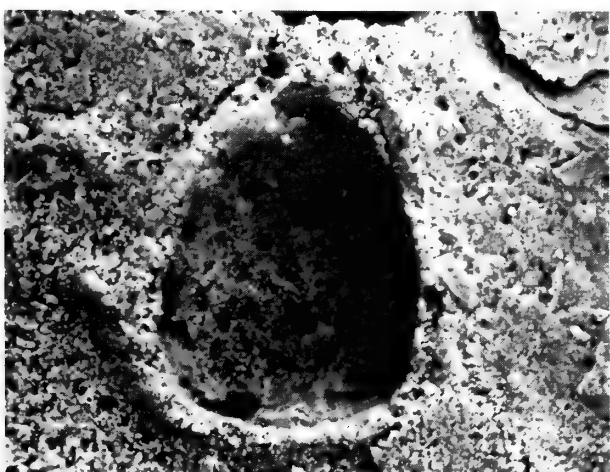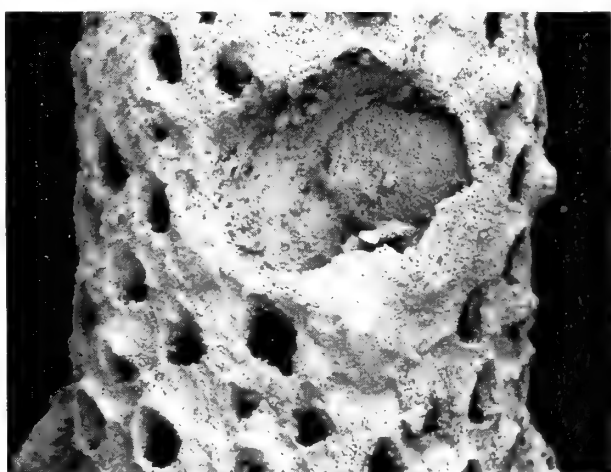
Figs 275–280 *Reptomultelea reussi* (Pergens, 1890). 275, 276, BMNH D36115, Cenomanian, Untere Planer, Plauen, Dresden, Germany; 275, autozooids and eleozooids, × 50; 276, autozooids with and without opercula and an eleozooid above, × 105. 277–279, VH 10428 Cenomanian, *plenus* Zone, Hoher Stein, Dresden-Plauen, Germany; 277, abraded growing edge, × 50; 278, eleozooidal aperture, × 240; 279, autozooidal aperture, × 240. 280, VH 10433, Cenomanian, *plenus* Zone, Hoher Stein, cavariiform colony with worn gonozooid, × 50.

Eleozooids (Figs 275, 276) abundant, scattered or clustered; small, frontal surface variable in size, usually significantly shorter and narrower than autozooids, and almost twice as long as wide; frontal wall occupying more than half of frontal surface, often somewhat depressed. Aperture (Fig. 278) equidimensional to more than 1·5 × longer than wide, variable in size, smaller than an autozooidal aperture, attaining maximum width between hinge line and mid-length, distally elevated and pointed often with concave margins where prolonged by rostral shelf; apertural shelf lacking; apertural rim raised, especially distally; hinge line apparently with short median bar. Operculum rarely preserved in-situ, flat, conspicuously depressed beneath level of apertural rim. Intramurally budded eleozooids within host eleozooids not observed.

Gonozooids represented by a single, poorly-preserved example (Fig. 280). Frontally a little longer than wide, distal dilated frontal wall rounded subtriangular in shape. Ooeciopore destroyed.

MEASUREMENTS.

autozooids (10 zooids from VH 10428)

frontal length:	mean = 0·53 mm; SD = 0·034 mm; CV = 6·4; range = 0·48–0·60 mm
frontal width:	mean = 0·27 mm; SD = 0·024 mm; CV = 8·9; range = 0·24–0·32 mm
apertural length:	mean = 0·20 mm; SD = 0·011 mm; CV = 5·2; range = 0·20–0·23 mm
apertural width:	mean = 0·16 mm; SD = 0·010 mm; CV = 6·3; range = 0·15–0·18 mm

eleozooids (10 zooids from VH 10428)

frontal length:	mean = 0·39 mm; SD = 0·085 mm; CV = 21·9; range = 0·30–0·57 mm
frontal width:	mean = 0·21 mm; SD = 0·027 mm; CV = 12·9; range = 0·17–0·26 mm
apertural length:	mean = 0·13 mm; SD = 0·041 mm; CV = 31·5; range = 0·08–0·20 mm
apertural width:	mean = 0·10 mm; SD = 0·017 mm; CV = 16·7; range = 0·08–0·12 mm

gonozooids (1 zooid from VH 10433)

frontal length:	*ca* 1·26 mm
distal frontal wall length:	*ca* 1·10 mm
frontal width:	*ca* 1·05 mm

REMARKS. Pergens (1890) proposed *Semielea reussi* as a new species to replace *Diastopora oceani* d'Orbigny *sensu* Reuss, 1872. His brief description is given only as a footnote to a revision of the Cretaceous cyclostomes figured by d'Orbigny (1851–54) in the 'Terrains Crétacés' and lacks any figures or mention of particular specimens. There is no evidence that he had any of his own material at hand when erecting this species. Therefore, the original specimens described by Reuss (1872) are taken as the syntypes of Pergens' new species. Unfortunately, the two figured syntypes of *S. reussi* (Reuss 1872: pl. 27, figs 2 and 3) are different species: the specimen shown in figure 2 (Voigt photocard 2814) is probably conspecific with *Reptomultelea sarthacensis* (d'Orbigny) (see p. 54); that shown in figure 3 (Voigt photocard 2166) is here chosen as the lectotype of *Reptomultelea reussi* (Pergens, 1890).

Pergens (1892) later provided a more complete description of *Semielea reussi* accompanied by a figure which shows a large eleozooid unlike those present in the lectotype of *S. reussi* but resembling the eleozooids of *R. sarthacensis*. This figure may be of a specimen, encrusting a sponge, from the Maastricht Museum which was on loan to Prof. E. Voigt when I had the opportunity to examine it in November 1987. This specimen is conspecific with *R. sarthacensis*. Two identified specimens of *S. reussi* were donated to the BMNH by Pergens and are registered as D36115 and D36116. The first is conspecific with the lectotype of *S. reussi*, whereas the second is indeterminate. It seems likely, therefore, that Pergens' concept of *S. reussi* was a broad one which included *R. sarthacensis* as well as *R. reussi*.

Reptomultelea reussi is readily distinguished by its small eleozooids with apertures of a similar shape to the autozooid apertures, except that they are prolonged distally by the presence of a short rostral shelf. Categorizing these eleozooids according to the tripartite classification of Taylor (1986*a*) is difficult; they are too small to be rostrozooids, lack the inverted T-shape of trifoliozooids, and are more pointed than demizooids. Perhaps they are best regarded as highly reduced rostrozooids.

None of the available material of *Reptomultelea reussi* is well-preserved; all specimens are variably abraded and have cement-obscured surfaces. Poor preservation partly explains the high variance of the eleozooidal dimensions, but a good deal of this variability is biological in origin.

Both the lectotype colony and specimen VH 10433 (Fig. 280) are cavariiform, thereby explaining Pergens' (1890, 1892) placement of the species in *Semielea* (see p. 42). Other specimens do not have such hollow growth-forms and assignment of the species to *Semielea* is therefore unjustified.

DISTRIBUTION. Upper Cenomanian (*plenus* Zone) of Dresden, Germany.

Reptomultelea sarissata Gregory, 1899   Figs 281–286

1899 *Reptomultelea sarissata* Gregory: 322, pl. 16, fig. 7.
1906 *Reptomultelea sarissata* Gregory; Lang: 63, fig. 9.
1912 *Meliceritites sarissata* (Gregory); Levinsen: 40, pl. 2, figs 1–3.

MATERIAL. Holotype: BMNH D7106 (main specimen plus two fragments), Upper Chalk, Beachy Head, Sussex, Gregory Colln.

Other material: BMNH D8011 (main specimen plus two fragments), D8012, [Coniacian], *cortestudinarium* Zone, Seaford, Sussex, Brydone Colln. BMNH D8568, D8576, [Coniacian], *cortestudinarium* Zone, Luton, Chatham, Kent, Gamble Colln. BMNH D11020, D11224, [?Coniacian], top of *cortestudinarium* Zone or base of *coranguinum* Zone, Chatham, Kent, Gamble Colln. BMNH D26835–9, D27022–4, [Coniacian], *cortestudinarium* Zone, Worms Heath, Surrey. BMNH D43661–2, [Coniacian], *cortestudinarium* Zone, Seaford Head, Sussex, Rowe Colln. BMNH D46891, Upper Chalk, Seaford, Sussex, Stuart Colln. BMNH D59276, [Coniacian], *cortestudinarium* Zone, Luton, Chatham, Kent, Rowe Colln. BMNH D58929 (7 fragments), Coniacian/Santonian, *decipiens* Zone Chalk, Vattetot-sur-mer, Seine-Maritime, France, Taylor & Hammond Colln. ZMC M35, Chalk, 'Chatham or Luton', Gamble Colln (specimen, on a flint, figd by Levinsen, 1912: pl. 2, figs 1–3). VH un-numbered: Coniacian, Fécamp, Seine-Maritime, France; Coniacian, Vattetot-sur-mer, Seine Maritime, France.

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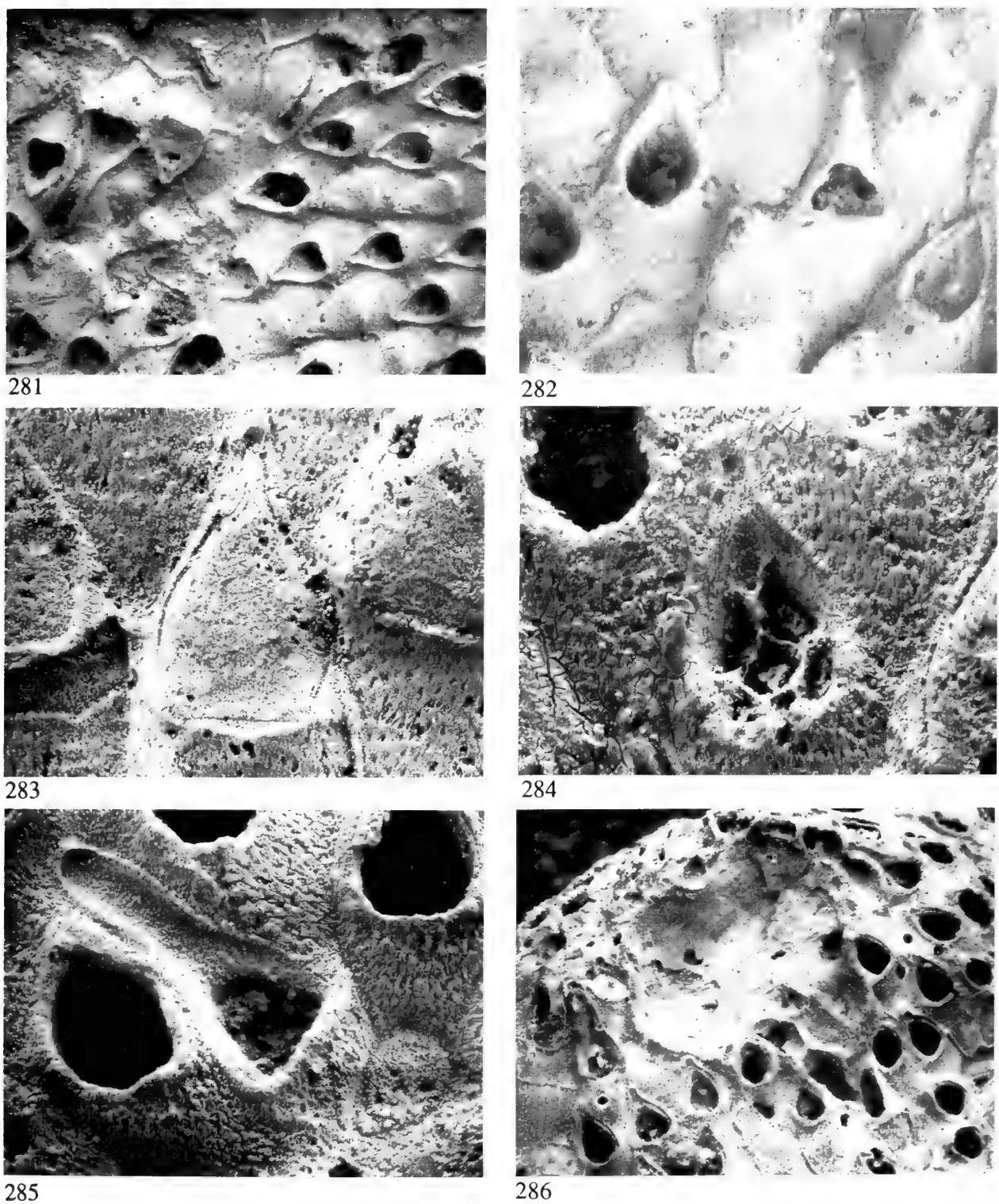
Figs 281–286 *Reptomultelea sarissata* Gregory, 1899. 281–282, BMNH D46891, Upper Chalk, Seaford, Sussex, 281, area of coalescent growth with autozooids, kenozooids and eleozooids, × 20; 282, autozooids and eleozooid with a broken operculum, × 48. 283–285, BMNH D7106, holotype, Upper Chalk, Beachy Head, Sussex; 283, autozooidal operculum, × 105; 284, autozooidal aperture showing intrazooecial fission, × 95; 285, eleozooid budded from a pseudoancestrula (lower right), × 77. 286, BMNH D8568, [Coniacian], *cortestudinarium* Zone, Luton, Chatham, Kent, crushed gonozooid, × 23.

DESCRIPTION. Colony unilamellar or multilamellar, each layer about 0·35 mm thick, layers sometimes growing freely with an exposed basal lamina. Overgrowths originate through intrazooecial fission (Fig. 284); pseudoancestrula an autozooid with aperture about 0·21 mm long by 0·17 mm wide; peri-pseudoancestrular buds may include autozooids, eleozooids (Fig. 285) or gonozooids, initiating secondary zone of astogenetic change during which apertural size increases and apertures become more pointed. Organization fixed-walled. Zooidal apertures arranged in quincunx except where disrupted near overgrowth origins and anastomoses.

Autozooids (Figs 281–282) very large, frontally elongate, generally 2–3 × longer than wide, hexagonal in outline, pointed distally; frontal wall convex, pseudopores slightly longitudinally elongate; boundary wall salient, often inconspicuous. Aperture (Fig. 284) of large size, longitudinally elongate, on average 1·6 × longer than wide, ogee arch-shaped with a short but distinct distal prolongation with concave sides, attaining maximum width between hinge line and mid-length; apertural rim salient; apertural shelf narrow, tapering proximally; hinge line with a median bar, teeth ?present. Operculum (Fig. 283) often preserved in-situ, convex; pseudopores not visible, probably as a result of poor preservation. Terminal diaphragms and intramural buds not observed.

Kenozooids occasionally present, usually located at overgrowth anastomoses (Fig. 281).

Eleozooids (Figs 281, 285) common; frontally very large, elongate, 2–3 × longer than wide, longer and generally a little wider than the autozooids. Aperture elongate, widest proximally at level of hinge line, narrowing with appearance of rostral shelf to become parallel-sided or very slightly spatulate, rounded and depressed distally. Opercula sometimes preserved in-situ, convex, pseudopores not visible, probably as a result of poor preservation. Intramurally budded eleozooids observed; apertures shorter than those of host eleozooid and less depressed distally.

Gonozooids (Fig. 286) represented by a single, broken example budded from a pseudoancestrula. Frontally pear-shaped, dilated frontal wall about 1·3 × longer than wide. Proximal floor showing outlines of underlying zooids, distal wall smooth. Ooeciopore damaged in available material. Atrial ring present.

MEASUREMENTS.
autozooids (10 zooids from holotype BMNH D7106)

frontal length:	mean = 0·92 mm; SD = 0·134 mm; CV = 14·6; range = 0·78–1·11 mm
frontal width:	mean = 0·38 mm; SD = 0·038 mm; CV = 10·2; range = 0·30–0·44 mm
apertural length:	mean = 0·40 mm; SD = 0·020 mm; CV = 5·0; range = 0·36–0·44 mm
apertural width:	mean = 0·24 mm; SD = 0·014 mm; CV = 5·7; range = 0·23–0·27 mm

eleozooids
(3 zooids from holotype BMNH D7106)

frontal length:	range = 1·32–1·44 mm
frontal width:	range = 0·48–0·51 mm
apertural length:	range = 0·72–0·83 mm
apertural width:	range = 0·32–0·36 mm

(7 zooids from BMNH D8011)
frontal length: mean = 1·16 mm; SD = 0·040 mm; CV = 3·4; range = 1·13–1·22 mm

frontal width:	mean = 0·45 mm; SD = 0·039 mm; CV = 8·8; range = 0·41–0·51 mm
apertural length:	mean = 0·73 mm; SD = 0·031 mm; CV = 4·3; range = 0·69–0·78 mm
apertural width:	mean = 0·33 mm; SD = 0·013 mm; CV = 4·1; range = 0·32–0·35 mm

gonozooids (1 zooid from BMNH D8568)

frontal length:	2·13 mm
distal frontal wall length:	1·97 mm
frontal width:	1·61 mm
ooeciopore width:	*ca* 0·15 mm (broken)

REMARKS. *Reptomultelea sarissata* is a very distinctive species readily recognized by the large, ogee arch-shaped autozooidal apertures. Eleozooidal morphology suggests affinities with *R. dixoni* (Lang) (see p. 69), which also has large autozooids. *R. sarissata* probably has a stratigraphical range restricted to the Coniacian (*cortestudinarium* Zone and equivalents).

Like other species of *Reptomultelea* from chalk facies, colonies are generally nodular to lamellar in shape and often appear to have been attached to soft-bodied organisms whose traces may remain as poorly-defined bioimmurations on the undersides of colonies.

DISTRIBUTION. Coniacian (?basal Santonian) of southern England and northern France.

Reptomultelea scanica sp. nov.   Figs 287–296

MATERIAL. Holotype: VH 10441, Lower Campanian, *mammillatus* Zone, Karlshamn, Scania, Sweden. Paratype: VH 10442, 10549 (sample), same details as holotype.

NAME. After the provenance.

DESCRIPTION. Colony unilamellar or multilamellar (Fig. 290), each layer about 0·3 mm thick, usually with a transversely undulose basal lamina growing freely of the substratum. Overgrowths originate by intrazooecial fission; pseudoancestrula an autozooid, aperture about 0·10 mm wide; periancestrular buds commence a secondary zone of astogenetic change of increasing zooid size. Organization fixed-walled. apertures arranged in approximate quincunx away from overgrowth origins and anastomoses. Mural spines visible in proximal parts of zooids exposed on fractured edges of specimens.

Ancestrula, probably of this species (Fig. 288), fouling the basal lamina of VH 10442, short (length 0·48 mm) with large protoecium (width 0·38 mm), negligable distal ancestrular tube, and aperture 0·15 mm long by 0·14 mm wide. Operculum not preserved, although presence of a straight hinge line implies that ancestrula was originally operculate.

Autozooids (Figs 289) small, frontally elongate, usually less than twice as long as wide and subrhomboidal in outline shape, rounded distally; frontal wall slightly convex, pseudopores subcircular; boundary wall salient but inconspicuous and mainly comprising apertural rims. Aperture (Fig. 291) of moderate size, occupying about half of the frontal area, longitudinally elongate, 1·1–1·3 × longer than wide, rounded distally, attaining maximum width between the hinge line and mid-length; apertural rim often thickened at proximolateral corners of aperture; hinge line with short median bar between low (?)teeth; apertural shelf broad
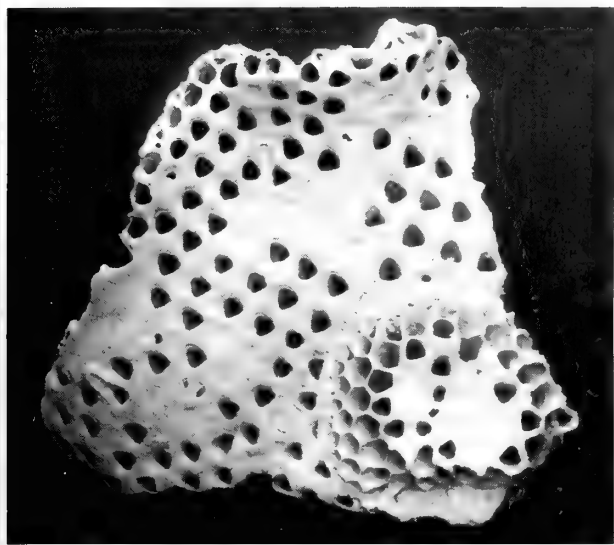
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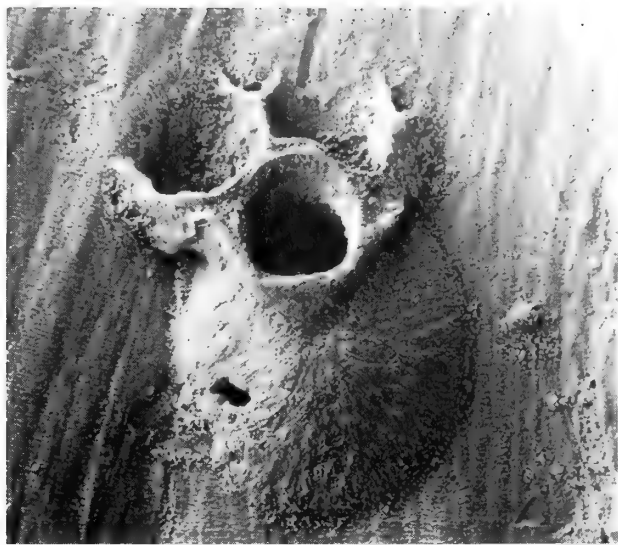
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Figs 287–288 *Reptomultelea scanica* sp. nov., Lower Campanian, *mammillatus* Zone, Karlshamn, Scania, Sweden. 287, VH 10441, holotype, colony fragment with newly-developed overgrowth (lower right), × 17. 288, VH 10442, ancestrula (presumed to be of this species) fouling underside of main colony, × 88.

distally, tapering proximally and disappearing at about the level of maximum aperture width. Operculum (Fig. 293) often preserved in-situ, convex; pseudopores radially elongate, scattered all over surface of operculum. Terminal diaphragms (Fig. 294) observed just proximal of apertural shelf, apparently lacking pseudopores. Intramurally budded autozooids probably represented by zooids with smaller opercula and thicker apertural rims.

Kenozooids rare, sometimes developed immediately distal of eleozooids.

Eleozooids (Figs 289, 295) moderately common, scattered, frontally elongate, about 2·5 × longer than wide, longer and wider than the autozooids, well-rounded distally. Aperture longitudinally elongate, generally 2·5 × longer than wide, distally parallel-sided or slightly spatulate and rounded; rostrum forming an extensive platform; apertural rim raised. Opercula not observed in-situ. Intramural buds and terminal diaphragms unknown.

Gonozooids known from a single example (Fig. 296). Frontally elongate, twice as long as wide, a short parallel-sided tube emerging from the maternal aperture and dilating into a longitudinally ovoidal shape. Autozooids adjacent to distal part of gonozooid are orientated parallel to margins of gonozooid. Ooeciopore transversely elliptical, twice as wide as long. Atrial ring not observed.

MEASUREMENTS.

autozooids (10 zooids with in-situ opercula from holotype VH 10441)

frontal length: mean = 0·44 mm; SD = 0·023 mm; CV = 5·5; range = 0·39–0·47 mm

frontal width: mean = 0·24 mm; SD = 0·014 mm; CV = 5·9; range = 0·23–0·26 mm

apertural length: mean = 0·20 mm; SD = 0·006 mm; CV = 3·2; range = 0·20–0·21 mm

apertural width: mean = 0·17 mm; SD = 0·009 mm; CV = 5·6; range = 0·15–0·18 mm

eleozooids (3 zooids from holotype VH 10441 and 3 zooids from VH 10442)

frontal length: mean = 0·76 mm; SD = 0·080 mm; CV = 10·5; range = 0·65–0·87 mm

frontal width: mean = 0·30 mm; SD = 0·013 mm; CV = 4·5; range = 0·29–0·32 mm

apertural length: mean = 0·44 mm; SD = 0·048 mm; CV = 10·9; range = 0·39–0·50 mm

apertural width: mean = 0·18 mm; SD = 0·011 mm; CV = 6·2; range = 0·17–0·20 mm

gonozooids (1 zooid from VH 10442)

frontal length: 1·80 mm

distal frontal wall length: 1·64 mm

frontal width: 0·90 mm

ooeciopore length: 0·09 mm

ooeciopore width: 0·18 mm

REMARKS. The youngest known species of *Reptomultelea*, *R. scanica* is characterized by its spatulate eleozooids, high autozooidal apertures which occupy about half of the frontal area of the zooid, and pseudopores distributed across the entire surface of the autozooidal opercula. Eleozooid shape is similar to *R. filiozati* (Levinsen), while the distribution of opercular pseudopores is reminiscent of *R. goldfussi* sp. nov., but other characters ensure that neither of these species could be confused with *R. scanica*.

Available specimens are small fragments of larger colonies. With the exception of one specimen which encrusts a shell fragment (?brachiopod), original substrates are not preserved and the basal lamina evidently grew freely into space. The shell-encrusting colony shows the beginnings of cavariiform growth.

DISTRIBUTION. Lower Campanian of Scania, Sweden.
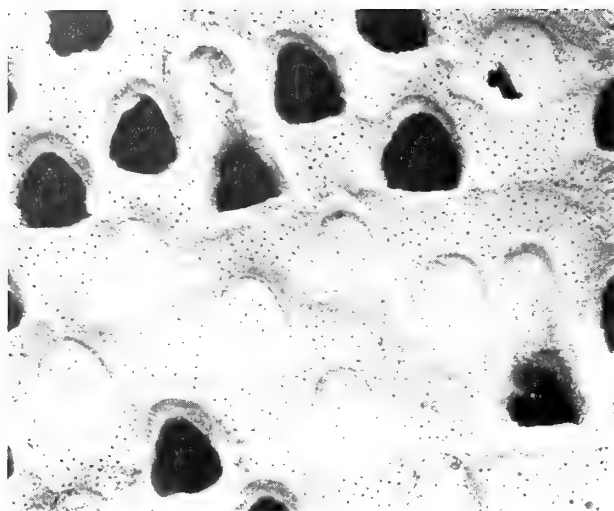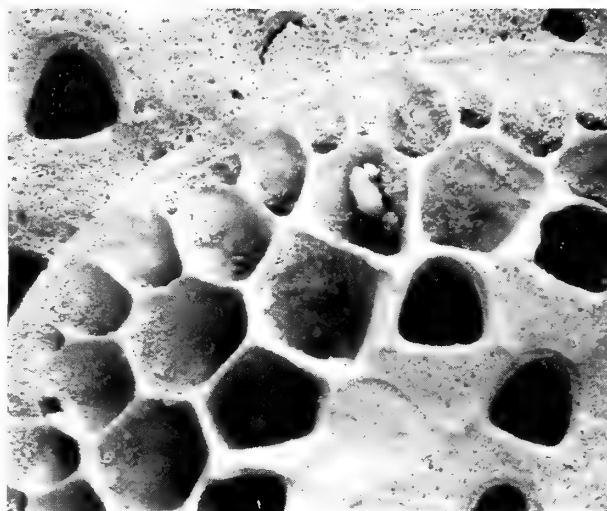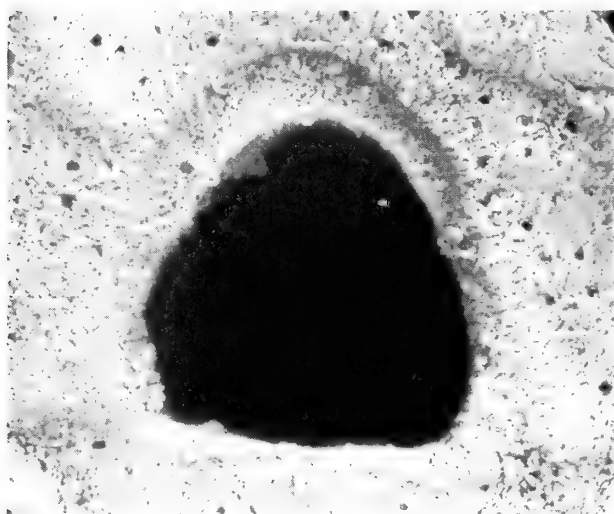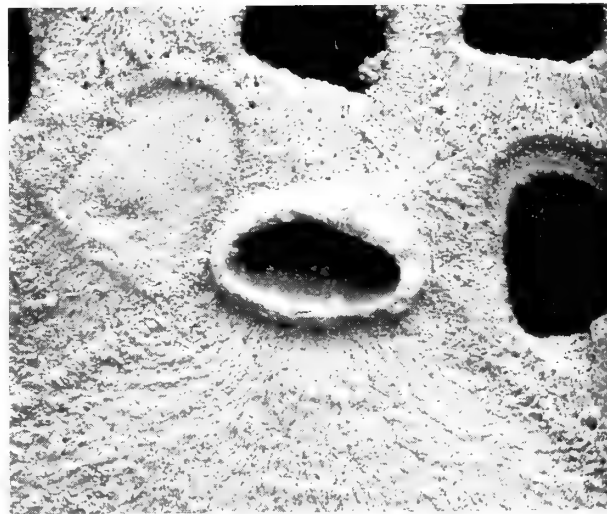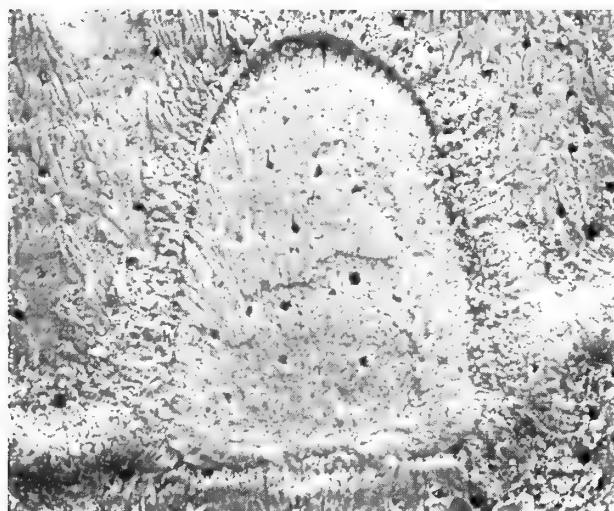
Figs 289–294 *Reptomultelea scanica* sp. nov., Lower Campanian, *mammillatus* Zone, Karlshamn, Scania, Sweden. 289–291, VH 10441, holotype; 289, autozooids and two eleozooids, × 67; 290, growing edge of overgrowth, × 74; 291, autozooidal aperture, × 270. 292–294, VH 10442; 292, ooeciopore, × 130; 293, autozooidal operculum, × 275; 294, autozooidal aperture with terminal diaphragm, × 270.

Fig. 295 *Reptomultelea scanica* sp. nov., VH 10441, holotype, Lower Campanian, *mammillatus* Zone, Karlshamn, Scania, Sweden, eleozooid, × 135.

Reptomultelea tuberculata (d'Orbigny, 1853)
Figs 297–302

1853 *Clausimultelea tuberculata* d'Orbigny: 656, pl. 784, figs 12–15.
1890 *Clausimultelea tuberculata* d'Orbigny; Pergens: 398.
1899 *Clausimultelea tuberculata* d'Orbigny; Gregory: 405.
1912 *Meliceritites tuberculata* (d'Orbigny); Levinsen: 35, pl. 6, figs 1–3.

MATERIAL. Holotype: MNHN d'Orbigny Collection 8203 (Voigt photocard 3717), Senonian, Triquerville, Seine-Inférieure, France.

Other material: BMNH D54295, Santonian, Evreux, Eure, France, Voigt Colln. VH un-numbered material: Coniacian, Fécamp; Coniacian, Vattetot-sur-Mer; Santonian, Evreux; Santonian (*coranguinum* Zone), Aulnay-sur-Iton.

DESCRIPTION. Colony multilamellar, each layer about 0·3 mm thick, growing as a series of discoidal subcolonies. Overgrowths originate through intrazooecial fission; pseudoancestrulae are autozooids and are followed by a secondary zone of astogenetic change. Organization fixed-walled. Zooidal apertures variably arranged.

Autozooids (Fig. 297) of medium size, frontally elongate, on average a little less than twice as long as wide, often hexagonal in outline with distal margin prolonged by the aperture; boundary wall salient. Aperture (Fig. 299) of moderate size, very tall, 1·5 × longer than wide, attaining maximum width between the hinge line and mid-length, rounded distally; apertural rim raised; apertural shelf moder-
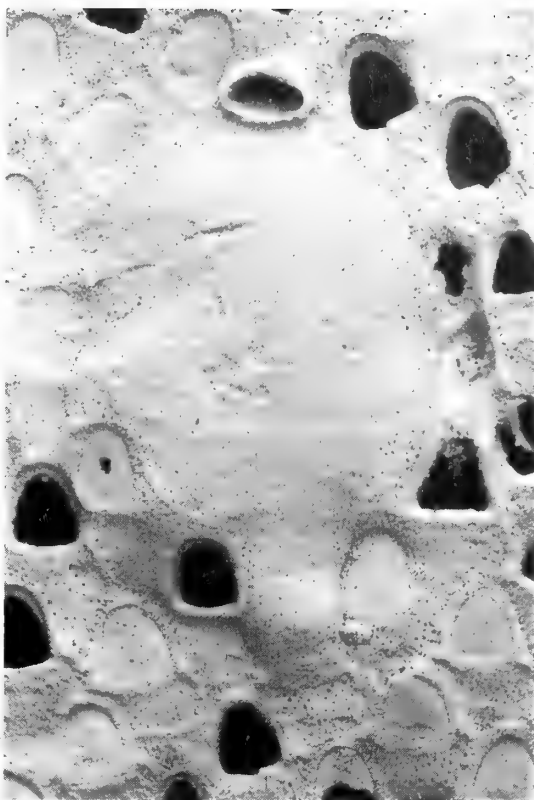
Fig. 296 *Reptomultelea scanica* sp. nov., VH 10442, Lower Campanian, *mammillatus* Zone, Karlshamn, Scania, Sweden, gonozooid, × 58.

ately wide, tapering proximally; hinge line with a median bar and ?teeth. Operculum (Fig. 298) convex; pseudopores number about 18 arranged in a crescent. Terminal diaphragms not observed. Intramurally budded eleozooids (Fig. 300) present within many autozooids; aperture similar in shape but shorter than those of primary eleozooids, a little raised distally, an area of calcification intervening between hinge line of host zooid and proximal edge of eleozooid aperture; operculum not observed.

Kenozooids (Figs 297, 301) numerous, intercalated between the other zooids and sometimes completely surrounding them.

Eleozooids (Figs 297, 301) common, elongate, about twice as long as wide, a little longer and narrower than the autozooids, distal outline narrow where prolonged by aperture. Aperture (Fig. 302) elongate, narrow, about 3 × longer than wide, attaining maximum width at the level of the hinge line, slightly indented laterally by rostral shelf between hinge line and mid-length, distally pointed and slightly raised. Opercula not observed in-situ. Intramural buds not seen within eleozooids.

Gonozooids unknown.

MEASUREMENTS.
autozooids (10 zooids with in-situ opercula from BMNH D54295)
frontal length: mean = 0·54 mm; SD = 0·046 mm;
                            CV = 8·6; range = 0·47–0·65 mm
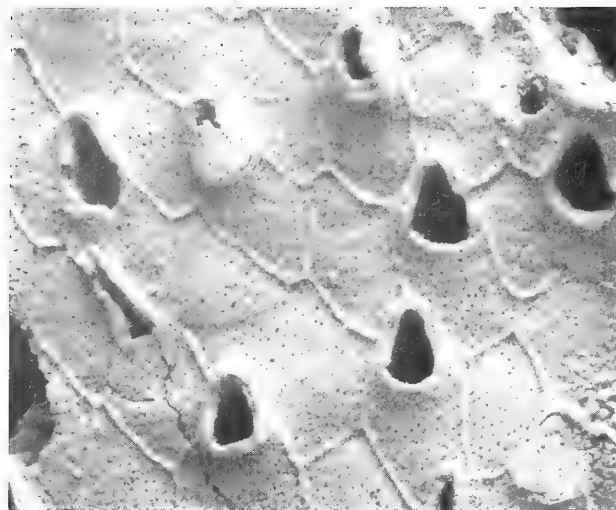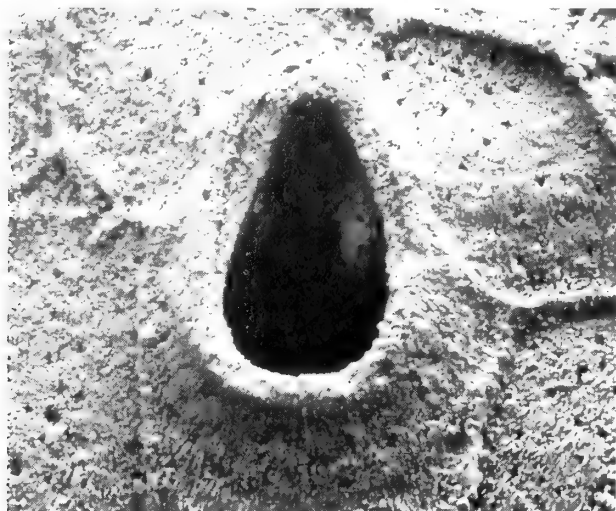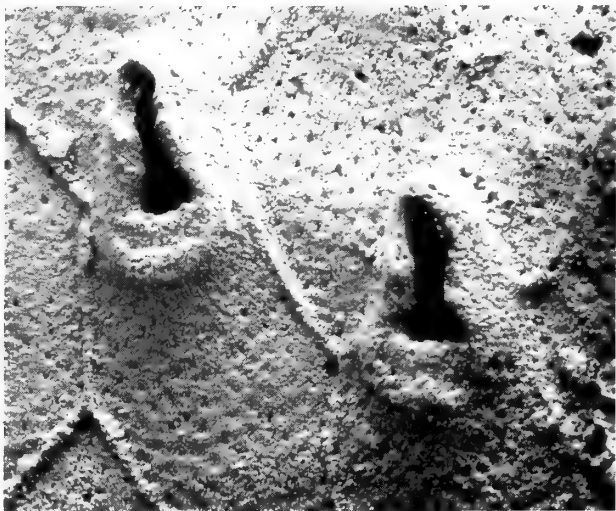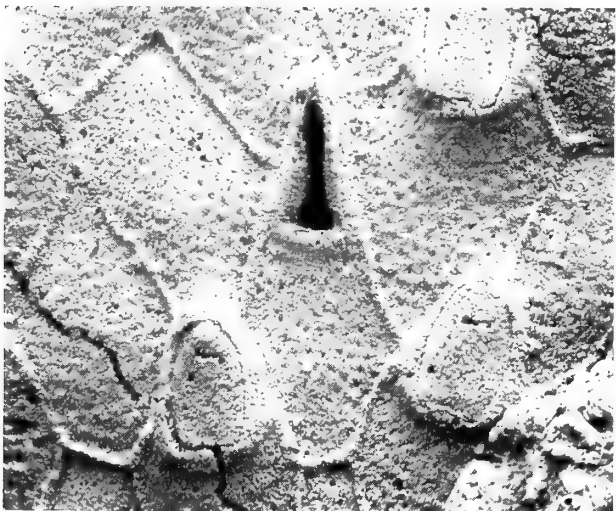
Figs 297–302 *Reptomultelea tuberculata* (d'Orbigny, 1853), BMNH D54295, Santonian, Evreux, Eure, France; 297, autozooids, eleozooids and kenozooids, × 60; 298, autozooidal operculum, × 225; 299, autozooidal aperture, × 225; 300, two intramural eleozooids, × 140; 301, eleozooid surrounded by operculate autozooids and kenozooids, × 105; 302, eleozooidal aperture, × 240.

Frontal width: mean = 0·29 mm; SD = 0·023 mm;
CV = 7·8; range = 0·24–0·32 mm

apertural length: mean = 0·21 mm; SD = 0·010 mm;
CV = 4·7; range = 0·20–0·23 mm

apertural width: mean = 0·14 mm; SD = 0·011 mm;
CV = 7·4; range = 0·12–0·15 mm

eleozooids (4 zooids from BMNH D54295)

frontal length: range = 0·54–0·65 mm
frontal width: range = 0·26–0·30 mm
apertural length: range = 0·18–0·26 mm
apertural width: range = 0·08 mm

REMARKS. *Clausimultelea tuberculata* d'Orbigny, 1853 is the type species by monotypy of *Clausimultelea* d'Orbigny, 1853, a genus here placed in synonymy with *Reptomultelea* (see p. 46). The narrow, acuminate apertures of the eleozooids, numerous kenozooids and high autozooidal apertures are useful features in identification of the species. The eleozooids invite comparison with *Meliceritites gothica* and similar species; a functional, if not phylogenetic, connection seems possible.

The only specimen of *Reptomultelea tuberculata* in the d'Orbigny Collection is a large colony reaching 50 mm in diameter and preserved on the outside of a flint. This specimen has been labelled 'Type' by E. Voigt and corresponds well with d'Orbigny's plate 784, fig. 12. Levinsen's (1912) material of *R. tuberculata* could not be positively identified among his collection of meliceritids in the ZMC, although this collection does include a specimen from Fécamp labelled '*Clausimultelea* n. sp.'. The record of *R. tuberculata* given by Levinsen (p. 36) from the Danian of the Paris Basin is highly doubtful as the genus *Reptomultelea* is not known to range above the Campanian.

DISTRIBUTION. Coniacian to Santonian of France.

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The brachiopods of the Duncannon Group (Middle-Upper Ordovician) of southeast Ireland

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CONTENTS

SYNOPSIS. Brachiopod assemblages from localities within the Duncannon Group of the Leinster terrane, southeast Ireland, are systematically described and figured. The localities were known to 19th century geologists but have been largely ignored since then. Re-collection permits a revised correlation between the Leinster localities and successions of adjacent terranes. The faunal assemblages are all of Caradoc age. Kildare (Grange Hill), Ballygarvan Bridge, Greenville-Moyne, Ballykale, Carrigadaggan and Kilbride are all probably Longvillian, whilst the faunas from Kildare Grange Hill House Cottage, Clologe, Greenville and Raheen are of probable Soudleyan, or possibly Harnagian, age. Brachiopods dominate the Duncannon faunas. One new species, *Petrocrania harperi* and one new subspecies, *Leptestiina oepiki ampla* are described.

The brachiopods are closely related to coeval Anglo-Welsh Province faunas, with many conspecific forms. The origins of the genera can be found mainly in earlier migrations of Baltic Province genera, although some Scoto-Appalachian genera are present as early immigrants, implying a mid-Ordovician phase of breakdown of Iapetus brachiopod provinciality. The faunas occur in volcano-sedimentary sequences, reflecting their palaeogeographical position in a volcanic arc marginal to the Eastern Avalonia microcontinent. This moved northward throughout the Ordovician, acting as a staging post for inter-provincial migrations, until its collision with Baltica and Laurentia.

Comparison of the assemblages reveals no direct similarities with Welsh palaeocommunities, although strong inter-locality resemblance is noted, despite the occurrence of varied lithologies. Except for the molluscan-dominated Soudleyan Kildare fauna, which resembles that at Herbertstown, assemblages indicate a normal marine environment in moderate to deep water surrounding volcanic centres.

INTRODUCTION

This work presents the results of re-collection and re-examination of many fossiliferous localities within the late Llandeilo and Caradoc strata of southeast Ireland. The area of research is confined to the NE–SW Caledonide trending belt of volcanic and sedimentary rocks of the Duncannon Group, extending from Co. Wicklow through Co. Wexford to south Co. Waterford; it also includes the peripheral Kildare inlier of Co. Kildare. The faunas are all early to middle Caradoc in age, and they are dominated mainly by brachiopods, with components of trilobites, gastropods, bivalves, bryozoans, crinoids, cystoids and orthocones.

Brachiopods are one of the most useful animal groups in Ordovician sequences for stratigraphical and environmental interpretation in non-graptolitic strata, so the emphasis of the present work is on their identification and description. Trilobites, although numerically a minor component of the faunas, are also discussed, but their detailed systematics will be presented separately by Dr A. Owen and this author. The preservation of almost all fossil material is as internal or external moulds and this makes identification of some elements, such as bryozoans, gastropods and bivalves, difficult. These elements are counted and listed in the relevant faunas,

but they are not identified or figured.

Limits of research area

With one exception, the boundaries of the Leinster terrane (Harper and Parkes 1989, Murphy *et al.* 1991) define the area, within which, outcrops of the various formations which make up the Duncannon Group were all examined. The rocks of the Tramore region south of Waterford were the subject of a Ph.D. research project by Hilary Carlisle at Queen's University, Belfast. Although an important paper (Carlisle 1979) summarized her main work, the Ph.D. thesis was never completed. The completion of the brachiopod systematics of the Tramore Limestone Formation is in progress by Carlisle, Dr D.A.T. Harper and the present author. The only locality from which her material was lost was Kilbride, in the Upper Tramore Volcanic Formation, and this important locality was re-collected.

The area of research, apart from the main belt of Duncannon Group rocks from Arklow through Gorey and Enniscorthy to the Waterford region, also takes in the Wicklow-Avoca volcanics and the Kildare inlier to the north-west (Fig. 1). Although the Ordovician greywackes of the Kilcullen Group to the west of the Leinster Granite, in west Wicklow, have yielded some fossils in the past, after literature research and a cursory reconnaissance, this area was not studied, since Brück (1971) has thoroughly revised the known Geological Survey of Ireland (G.S.I.) fossil localities.

Outside this area in the Iapetus suture zone of eastern Ireland, the present research has involved some restricted fieldwork and literature work to draw comparisons and contrasts between the faunas of the Leinster terrane and those of the Bellewstown and Grangegeeth terranes. The only case where detailed investigation has taken place involves a new record of shelly fossils in the Llanvirn Hilltown Formation of the Bellewstown terrane (Harper *et al.* 1991).

Revision of Duncannon Group faunas

In the Caledonides of western Europe and the eastern United States and Canada, many areas have been the subject of detailed modern palaeontological studies, often resulting in monographic treatment of the more important fauna. In the case of Wales, the Welsh Borderland and Girvan in Scotland, many Ordovician successions have been revised. These include the Bala area of North Wales (Williams 1963), the Shelve district of Shropshire (Williams 1974), Girvan in southwest Scotland (Williams 1962), Anglesey (Bates 1968), mid and southwest Wales (Lockley & Williams 1981, Williams *et al.* 1981), various areas of North Wales (Pickerill & Brenchley 1979, Lockley 1980, Hiller 1980 and Bates 1969) and the type upper Caradoc of Shropshire (Hurst 1979*a*).

Although some localities in Ireland have received modern taxonomic treatment, such as the Tourmakeady Limestone in Co. Mayo (Williams & Curry 1985) and the Portrane Limestone in north Co. Dublin (Wright 1963, 1964), the area considered here has received only partial revision and attention. Brenchley *et al.* (1977) completed a reappraisal of several Caradoc localities in eastern Ireland, including Slieveroe near Rathdrum, some sites around Enniscorthy (Greenville, Greenville-Moyne) and the successions at Bellewstown and Grangegeeth; their paper was a fundamental resource for the present work.

The present work repairs an omission in providing a modern description of the faunas in the southeast of Ireland, an area very poorly known by comparison with coeval successions in other parts of Ireland and Britain. In terms of biogeographical models the Leinster terrane occupies a pivotal position in cross Iapetus migrations, being the most external or marginal area of the Eastern Avalonia microcontinent and occupying a progessively more axial position within the closing Iapetus ocean in the Ordovician. As a chain of volcanic islands the Duncannon Group environments provided staging posts in the dispersal of shelly benthos with larval juvenile stages. The localities described herein are important in charting the migration of different species between the platform provinces of Laurentia, Baltica, Gondwana and the microcontinental terranes including Avalonia.

Although, with few exceptions, the existence of the faunas described here was known to geologists in the 19th century, progress in understanding palaeontological concepts and the concomitant increase in differentiation of species has been such that the faunal lists published by the early collectors are now of little more use than as a provisional guide. One 'species' of the 19th century may now be recognized as comprising three or four different genera. Examples include '*Leptaena sericea*' for plectambonitoid genera, '*Orthis calligramma*' for impunctate orthoid genera and '*Orthis testudinaria*' for punctate orthoids.

HISTORY OF RESEARCH

19th century research

The major reference to the faunas is that of M'Coy (1846), whose description of the fossils collected by many workers under the direction of Sir Richard Griffith (in his attempts to make the first geological map of Ireland) was done largely without knowledge of the localities or lithologies and was thus a considerable achievement. The efforts of Griffith, and his relationship with the official Ordnance Survey, as well as to the geological community in Ireland, is a fascinating story related by Herries Davies (1983), who has made clear that in many aspects the lead in geological mapping and thinking came from the G.S.I., and this affected progress in the Geological Surveys of England, Scotland and Wales.

In the 19th century some major works describing Irish geology and palaeontology included the third edition of *Siluria* (Murchison 1859) and Davidson's fine monographs of British 'Silurian' Brachiopoda (1853, 1866, 1867, 1869, 1871, 1883). In addition, noteworthy works include those of Reynolds & Gardiner on several specific areas including the Kildare Inlier (1896). Also important was Reed, who published papers on the Tramore area of Co. Waterford (1895, 1899, 1900).

1900–1950

After the initial mapping of Ireland was completed by the G.S.I. in 1890 with the publication of 1″ Sheet 10, there was very little new research of note or new interpretations in the following 70 years. In 1939 the Geologist's Association published a collection of papers on S.E. Ireland, including Hallissy (*in* Smyth, 1939) on the present study area. A

significant precursor to new investigations was a review paper by J.C. Harper (1948).

1950–1992

After the middle of the 20th century there were 3 main 'schools' of research developed in relation to the geology of S.E. Ireland that were important to this research.

J.C. Harper, based in Liverpool. Stemming from the interest and research of J.C. Harper in Irish Lower Palaeozoic geology, a series of papers by him and colleagues was presented. The most significant for this study is Brenchley *et al.* (1977), revising some successions in eastern Ireland based on new collections of fossils from Greenville, Enniscorthy, Slieveroe and Grangegeeth. Others of note are Harper & Rast (1964) on the Bellewstown succession; Crimes & Crossley (1968) and Brenchley & Treagus (1970) on the Courtown succession; Brenchley *et al.* (1967*b*) on the Tagoat faunas in the Rosslare terrane; Harper (1952) and Brenchley *et al.* (1967*a*) on the Grangegeeth inlier and Romano (1980*a*, 1980*b*) on the eastern Ireland Ordovician inliers. France (1967) also listed Caradoc fossils from Balbriggan.

Queen's University Belfast. A succession of work on Ordovician rocks in Leinster was also completed under the guidance of Alwyn Williams in Queen's University Belfast. Aside from Wright's researches at Kildare there was work by Carlisle (1979) on the Tramore area, Hiller (1971) on the Courtown rocks, and Mitchell (Mitchell *et al.* 1972) on both areas. Mitchell (1977) also subsequently completed a major revision of the Pomeroy inlier in Co. Tyrone.

Geological Survey of Ireland. Under G.S.I. instigation the Leinster area was remapped. Gardiner (1967) remapped the Duncannon area of S. Wexford and elucidated the structure (1970) and stratigraphy (1974) of the region. The area to the north but not adjoining, between Wexford and New Ross, was remapped by Shannon, who described the stratigraphy and sedimentology (1978, 1980), structure (1977, 1979*b*) and petrology (1979*a*). More recently the area to the north in Co. Wexford has been remapped by Geraghty (1989) and the area further north, extending to Co. Wicklow, was the subject of an M.Sc. thesis by Martinez (1987). This Wexford research and work by Downes (1974), Boland (1983) and Carlisle (1979) in the Tramore region have recently been compiled by the G.S.I. and new maps are in production. Also, Brück *et al.* (1978, 1979) refer to many publications based on aspects other than palaeontological research.

Recent research. This has been focussed on terrane tectonics and its application to understanding the development of the Irish Caledonides within the Iapetus Ocean (Murphy *et al.* 1991). Harper & Parkes (1989) have outlined the palaeontological constraints on the definition and development of Irish Caledonide terranes.

INFORMATION SOURCES FOR FOSSIL LOCALITIES

The primary source of information for tracing fossil localities in this study were the memoirs of the G.S.I., which list all fossiliferous sites encountered during the G.S.I. mapping programme in the mid 19th century. Locality information is restricted to a townland name (a townland is a small land

area) and a quarter sheet of the six inch (1:10560) series of topographic Ordnance Survey maps. However, some localities are misplaced.

Another primary source of data was M'Coy's (1846) *Synopsis of the Silurian Fossils of Ireland*. The locality information given by M'Coy was vague, with a townland name being the smallest area unit used to identify sites. This may explain why different faunas and lithologies were lumped together under one townland name. One of the main workers who collected for Griffith was John Kelly, who recognized that the locality information given by M'Coy was poor and gave more precise details of known localities (Kelly 1860).

Apart from these major sources, published works detailed in relevant sections provided further information, the most important of these being Brenchley *et al.* (1977). Significant information was obtained by direct contacts with other researchers and local farmers. The thoroughness of the G.S.I. mapping programme and of the other 19th century geologists is clearly shown by the fact that no new fossil localities were found despite extensive fieldwork.

LOCALITY INFORMATION BY 1″ GEOLOGICAL SURVEY OF IRELAND SHEET

Figure 1A shows the 1″ geological sheets examined completely or in part in this research. This section gives all relevant information on the fossil localities on each sheet, whether or not any collection was made by the author, and the current status of the site where known. Fig. 1B is a location map of the main localities collected, and the sections illustrated on Fig. 14 (p.126) plus other locations discussed in the text.

Sheet 119

The only Ordovician fossil localities on this sheet are discussed by Baily (*in* Jukes *et al.*, 1858). They all occur within the Kildare Inlier and have been revised (Parkes and Palmer 1994).

Sheet 120

Seven localities are listed in the memoir for this sheet (Hull 1880). They were all examined recently by Brück (1971) and dealt with thoroughly. No further work was attempted for this study, and no new localities are known.

Sheets 121 and 130

This memoir (Jukes & Du Noyer 1869) does not tabulate fossil localities. Four 'Lower Silurian' localities are referred to, all in the area of Rathdrum, Co. Wicklow.

(i) Rathdrum Hill, Kilcommon, Co. Wicklow, 30/1 or 3/30 (of the 6″ series) in grey sandy beds. This locality was not found on G.S.I. 6″ fieldsheets and no fossiliferous rocks were located in the area in reconnaissance fieldwork.

(ii) Quarry near Rathdrum Bridge, on road to Glenealy and Wicklow, townland of Glasnarget north, Co. Wicklow 30 (?) in cleaved slate. The locality details are somewhat vague and the site was not found on the G.S.I. 6″ fieldsheets, but is believed to be a quarry now occupied
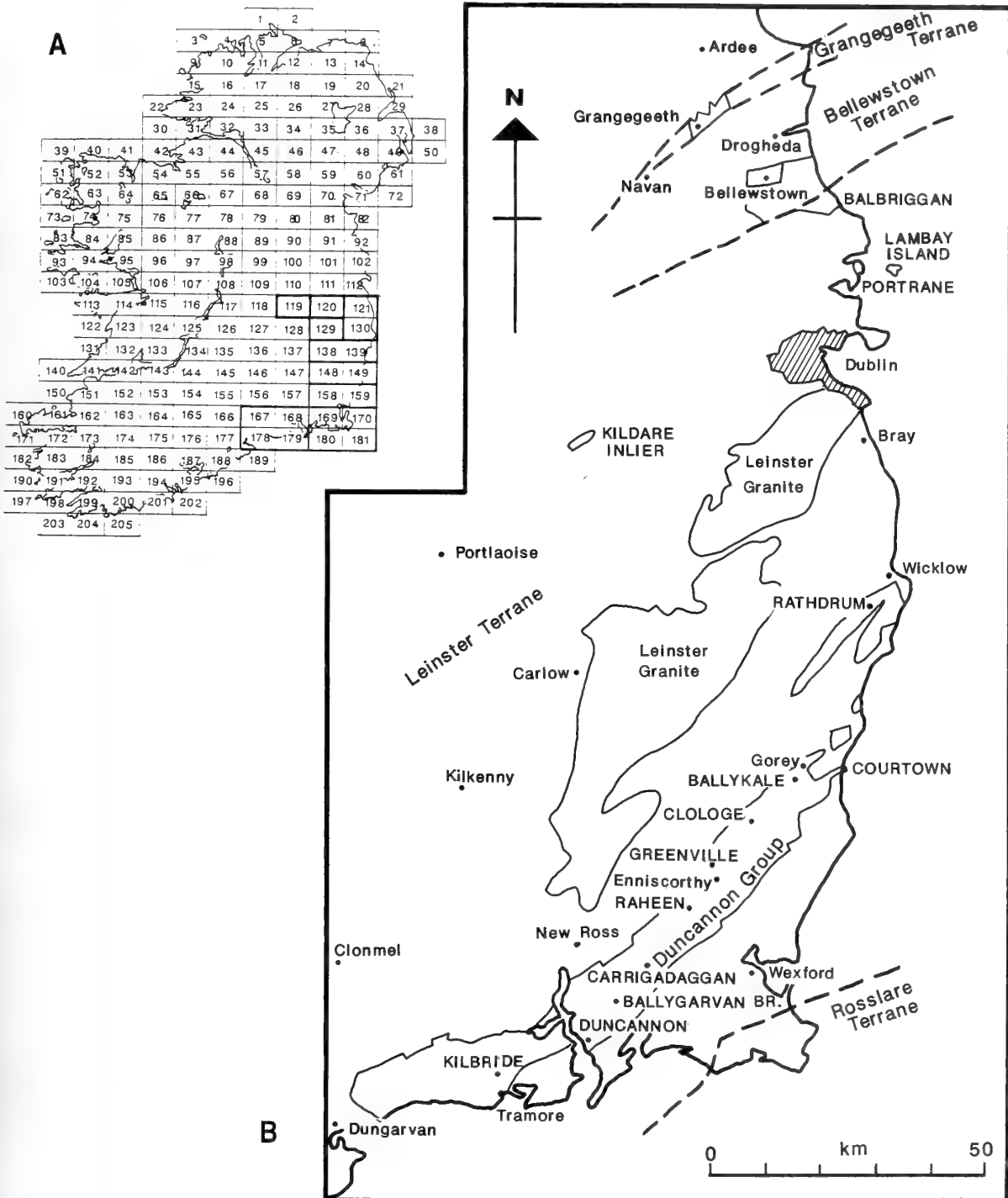
Fig. 1 A, index map of Geological Survey of Ireland 1-inch sheets examined in whole or part for revision of fossil localities. B, location map for the main sections shown on Fig. 14 (p. 126), and other localities in the Leinster terrane and adjoining terranes.

Table 1 Localities from G.S.I. Memoir examined in Sheets 148 and 149, with present status.

Loc. no.	¹/₄ sheet of 6″ map	County & townland	Situation & geological formation & 1″ map
		Wexford	Sheet 148
1	16/1	Clologe, Upper	From debris, in field close to road, from Norris Mount to Milltown, 1mile S of Camolin; light grey & brown slates, & tuffose rock. See later section.
2	20/1	Killabeg	Quarry on bank of R. Bann, 1 mile S of Clone Wood & 3 miles S of Ferns; black slates. Graptolite loc. – not examined.
3	20/2	Ballydonegan	On road from The Harrow to Tinnacross, 1 mile SW of The Harrow; grey shales. No exposure found here.
		Wexford	Sheet 149
4	7/4	Kildermot	See Courtown localities.
5	7/4	″	″
6	7/4	″	″
7	7/4	Ballymoney, Lr.	″
8	7/4	Seafield	″
9	11/2	Ballykale	See later section.
10	11/2	Coolnaveagh	About 2 miles S of Gorey a little W of Ballinatray Bridge; black slates. Not located.
11	11/3	Ballydaniel	One mile W of Balloughter; bluish grey compact altered rock. No fossils found here.
12	11/4	Clogh and	A little SE and SW of Clogh.
		Frankfort	See later section.
13	12/1	Ballinatray, Lr.	See Courtown localities.
14	12/1	″	″
15	12/1	″	″
16	12/1	Seamount	″
17	12/2	Duffcarrick	″
18	12/3	Coolnahinch	A little SW of Ballywalter House, 2·5 miles S of Gorey. Not traced.
19	12/4	Seamount	Graptolite locality in Ribband Group – not examined.

Table 2 Localities from the G.S.I. Memoir examined in Sheet 158, with present status.

Loc. no.	¹/₄ sheet of 6″ map	County & townland	Situation & geological formation & 1″ map
		Wexford	Sheet 158
1	19/4	Kiltrea	Graptolite loc. See Brenchley et al. (1967).
2	20/3	Moyne Upper	Quarry near road, a little S of Moyne House, 1·5 miles N of Enniscorthy; dark grey slates. Quarry now infilled – no exposure at all. See Brenchley et al. (1977) for faunal lists from collecting in that revision.
3	20/1	Moyne Lower	A little NE of Moyne House, 2 miles N of Enniscorthy; light bluish shales, weathering brown. No exposure at present.
4	20/3	Greenville & Moyne Upper	Old quarry, 1 mile N of Enniscorthy; dark grey shales. Fauna collected here in large blocks from newly ploughed strawberry field immediately adjacent to quarry. See later section.
5	20/3	Greenville	See later section.
6	20/3	Clonhasten & Ballynacarny boundary	Between Ballynabarny House and White's Bridge, 1·5 miles NE of Enniscorthy; dark grey slates. This site was not examined in this study or by Brenchley et al. (1977).
7	31/2	Ballybrennan	A little N of Ballybrennan House, 1·5 miles W of Clonmore, & about 6 miles SW of Enniscorthy; grey shales and grits. Shannon (1979a) recorded fossils here but no exposure is now available.
8	31/1	Raheen	Near Chapel Village, 6 miles SW of Enniscorthy; light grey shales & grits. See later section.

by a religious grotto about 100m from the bridge at Rathdrum. However, no fauna was found in the very slaty rock there.

(iii) Wicklow 30/3 one mile on road from Rathdrum to Redcross. This was considered too obscure and the supposed specimens too poor even in 1869 and no attempt was made to trace the locality in this study.

(iv) An old road cutting in the townland of Slieveroe, Co. Wicklow 30/1. This is discussed in brief below.

Sheet 129

The memoir for this sheet (Mitchell 1884) has one palaeontological note by W.H. Baily concerning the only known locality at Ballintaggart, Co. Kildare. This was examined by Brück (1971) in his examination of fossil localities west of the Leinster granite, and is not included here.

Sheets 138 and 139

Hull (1888), author of the G.S.I. memoir, mentions the only fossil locality in the text (p.8). A graptolite locality with poorly preserved forms 'allied to, or identical with *Graptolithus Sedgwickii*' was known a short distance NW of Arklow. The author has recently traced and curated these

Table 3 Localities from the G.S.I. Memoir examined in Sheet 168, with present status.

Loc. no.	¼ sheet of 6″ map	County & townland	Situation & geological formation & 1″ map
		Waterford	Sheet 168
1	9/4	Gibbet Hill	New road cutting on S side of R. Suir, a little NW of Waterford; black argillaceous slates. Graptolite locality, not examined.
2	17/4	Killure	Old quarry at the back of Farm House, 3 miles S of Waterford, on the road to Clohernagh Bridge; brown calcareous impure limestone. G.S.I. 6″ fieldsheets were not accessed for this area and it was not traced.
3	18/4	Raheen	Rocks on shore, a little N of Newtown Head, Waterford Harbour; dark grey concretionary shales. Owen et al. (1986) have revised the trilobite fauna. D.A.T. Harper is revising the brachiopod assemblage from here.

Table 4 Localities from the G.S.I. Memoir examined in Sheet 169, with present status.

Loc. no.	¼ sheet of 6″ map	County & townland	Situation & geological formation & 1″ map
		Wexford	Sheet 169
1	35/1 & 2	Carrigadaggan	About 1·5 miles SE of Ballynabola; grey shales. See later section.
2	35/4	Newbawn	A little N of Newbawn, 1·5 miles SE of preceding locality; grey shales. No fossiliferous exposure found here. A new quarry exposure with fossils was recently reported to me (pers. comm. M. Allen) but not visited in this research.
3	40/1	Ballygarvan	A little S of Ballygarvan Bridge, 3 miles SW of preceding locality; grey shales. See later section.
4	45/4	Ballymadder	Rocks on shore a little W of Ballymadder Point; dark grey shales. Reconnaisance visit only made here. No fossils located. Dan Tietzsch-Tyler (pers. comm. 1986) did not find significant fossils while mapping the area in detail.
5	45/4	Loftusacre	Rocks on shore W of preceding locality; grey micaceous and argillaceous shales. Same comment as loc. 4 applies.

specimens in the G.S.I. collections. They have been identified by Dr. A. Rushton, and indicate an early Ordovician, possibly Arenig age (John Morris G.S.I., pers. comm., 1994).

Sheets 148 and 149

This memoir (Hardman 1887) has palaeontological notes by W.H. Baily, who tabulated the localities. These are reproduced here with relevant information from this revision (Table 1).

Sheets 158 and 159

W.H. Baily contributed palaeontological information to this memoir (Kinahan 1882), again tabulating the fossil localities and listing the fossils collected. These are listed here with applicable information from this work (Table 2). All are from Sheet 158; none were known from Sheet 159.

Sheets 167, 168, 178 and 179

This memoir (Du Noyer 1865) also has palaeontological notes by W.H. Baily, who listed the fossils collected and tabulated the localities on Sheets 168, 178 and 179 (none were known from Sheet 167). The area of Sheet 167 is largely Caradoc or Silurian and has been studied by Penney (1980), who discussed recent faunal dating (p.319), including a Caradoc graptolite record from the Ross Formation. Sheet 178 to the west of the main Tramore volcanics is also outside the scope of this research as discussed in the Introduction. Similarly, Sheet 179 is all outside the confines of the present project and the subject of revision by D.A.T. Harper, H. Carlisle and

myself. The area is described by Carlisle (1979).

However, the Kilbride locality discussed below is within the confines of Sheet 179 and adjacent to localities 13–16. It is worth noting the confusion caused in the past by the similarity of the names of Newtown Head in Waterford Harbour (locality 3 – Raheen, but not the Raheen near Enniscorthy) and that of Newtown Cove, Great Newtown Head and Newtown Glen, all on the west side of Tramore Bay, fossiliferous strata being found at all locations. Sheet 168 contains three localities, shown in Table 3.

Sheets 169, 170, 180 and 181

Kinahan (1879) wrote the memoir to the four sheets covering southeast Co. Wexford, with W.H. Baily again contributing palaeontological information in tabulated form. Sheet 169 is the one relevant to this study. The table of 'Lower Silurian' localities is reproduced here with updated information (Table 4).

Sheet 170 has two listed localities which are part of the Rosslare terrane and whose faunas were described by Brenchley et al. (1967b). These are currently being reassessed by Harper & Bates (in prep). Sheet 180 has only one graptolite locality, visited but not yielding any specimens; recent workers have not found any trace of them and suggest the deformation is too strong to preserve fossils (Gardiner

1967: 6). Sheet 181 has no fossil localities at all.

A further significant point to note in connection with the composite list of fossils collected from these sheets is that in the sections on 'Lower Silurian' trilobites, brachiopods and graptolites many species are recorded from Locality 12. This is definitely a Carboniferous locality. According to the G.S.I. Map Curator, A.G. Sleeman (personal communication, 1988), these records are actually from Localities 16 and 17, which are both in the Tagoat area of the Rosslare terrane. He detailed many further complexities resulting from 'some rather sloppy curating going on in the 19th century'. These errors clearly show the need for caution in utilizing the existing faunal lists alone in modern interpretative work.

DETAILED LOCALITY INFORMATION

The Kildare Inlier, Co. Kildare (1:126720 – SHEET 16, N724175 – Horizons 1 & 2, N724179 – Grange Hill Cottage)

This inlier is described in detail elsewhere (Parkes and Palmer 1994). Only two main horizons and one minor one have been sampled extensively for the present work. All are of Caradoc age and on the flanks of the andesites of Grange Hill. The three localities sampled are shown in Fig. 2. The older fauna at the back of the ruined farm cottage, called Grange Hill House Cottage herein, is on the northern side of Grange Hill, on the edge of the common land. Grange Hill Horizons 1 and 2 are located only a few metres apart on the lowest slopes of Grange Hill in and just above an old obsolete field boundary.

The oldest reference to the inlier seems to be M'Coy (1846), who listed many of his species from 'the Chair of Kildare' (in the townland of Carrickanearla). This has led to much subsequent confusion since the townland includes rocks of Caradoc and Ashgill age and fossils from different horizons were treated together.

In 1858 the G.S.I. memoir to Sheet 119 (35 NE) was published (Jukes *et al.* 1858). A separate list was given for fossils found at Grange Hill House Cottage, but the identifications were not indicative of significant differences between that locality and the combination list for the Kildare Limestone and Grange Hill. These fossils have never been described although Williams *et al.* (1972) stated it was a Soudleyan fauna. Wright (1970) published a study of the inarticulate brachiopod *Orthisocrania divaricata*, which is found only in the Caradoc siltstones dated as Longvillian on the basis of faunal similarity with the Gelli-grîn Group of Bala in North Wales. Wright's list is the only modern reference to the Grange Hill (Horizons 1 & 2) fauna, which is described fully herein.

Kilbride and adjacent localities, Co. Waterford (1:126720 – SHEET 23, S578050)

The Kilbride locality is not a G.S.I. nor a Griffith locality but is one of the few recently discovered fossil sites in the area. It was found and collected first by Hilary Carlisle in the course of her doctoral research. Carlisle (1979) described the stratigraphy of the Tramore area, Co. Waterford, and listed the genera from Kilbride. Although Carlisle's work was never

completed, the material she collected was largely saved by Dr D.A.T. Harper with the intention that they should jointly complete the taxonomic study of the Tramore faunas. Although the Tramore Limestone Formation collection is currently under study by Harper, Carlisle and myself, the Kilbride material was lost. Extensive re-collection of this stratigraphically significant locality in the Upper Tramore Volcanic Formation was a high priority in the present study. The locality is shown in Fig. 3 and a detailed survey of the quarry is shown in Fig. 4, which pinpoints the position from which the re-collection was made.

In Du Noyer (1865:18) four localities are listed by Baily which are adjacent to Kilbride on 1" Sheet 179. These are Towergare (13 & 16), Munmahoge and Lisduggan (14) and Munmahoge (15), all townlands half a mile north of Kilbride. For all four localities the memoir descriptions are vague. Recourse to the 6" G.S.I. fieldsheets was necessary since the localities are not even indicated on the 1" Sheet 179. The original fieldsheets have been replaced by photographic copies in the G.S.I. and only limited information could be obtained. Munmahoge (15) was examined closely but the other localities were not traced. No fossiliferous exposures were found. However, the faunal lists are short with only three or four species other than the ubiquitous bryozoan 'Stenopora fibrosa', although at Munmahoge (15) abundant specimens are indicated.

Ballykale, Co. Wexford (1:126720 – SHEET 19, T147570)

This locality was recorded as a G.S.I. locality (No. 9) in the Sheet 149 memoir (Hardman 1887). It was noted as being 'one mile and a half south of Gorey; tuffose rock'. The quarter Sheet 11/2 of the G.S.I. fieldsheets showed the locality, although it is possible to confuse it with any of several adjacent localities such as Coolnaveagh (No. 10), Coolnahinch (No.18), or a number of other sites indicated by asterisks on the 1" Sheet 149, which are not easily correlated with the memoir table.

Kelly (1860) noted the locality as being '2 miles south of Gorey, on the east side of the road. The locality is nearly surrounded by a felspathic protrusion of yellow rock, such as is frequent thereabouts'. The actual position of the collection made by me is shown in Fig. 5. The locality has received no attention since the G.S.I. memoir. Field investigation did not reveal any exposure, but one large block in the base of the wall bounding the farm road was found to be packed with fossils, a nearly monospecific assemblage of *Bimuria* cf. *dyfiensis* Lockley (p.155). Although not *in situ* it is believed to be of local origin. The rock is a very tuffaceous mudstone and has been relatively strongly deformed, but the flattened fossil moulds are clearly identifiable.

Clologe Upper, Co. Wexford (1:126720 – SHEET 19, T051509)

As locality 1 in the memoir for Sheet 148 (Hardman 1887), this site was also identified clearly on the G.S.I. 6" fieldsheets, on quarter Sheet 16/1 of Co. Wexford. The memoir records that fossils came 'from debris, in a field close to the road from Norris Mount to Milltown, one mile south of Camolin; light gray and brown slates, and tuffose rock'. Re-investigation of the area, shown on Fig. 6, failed to locate
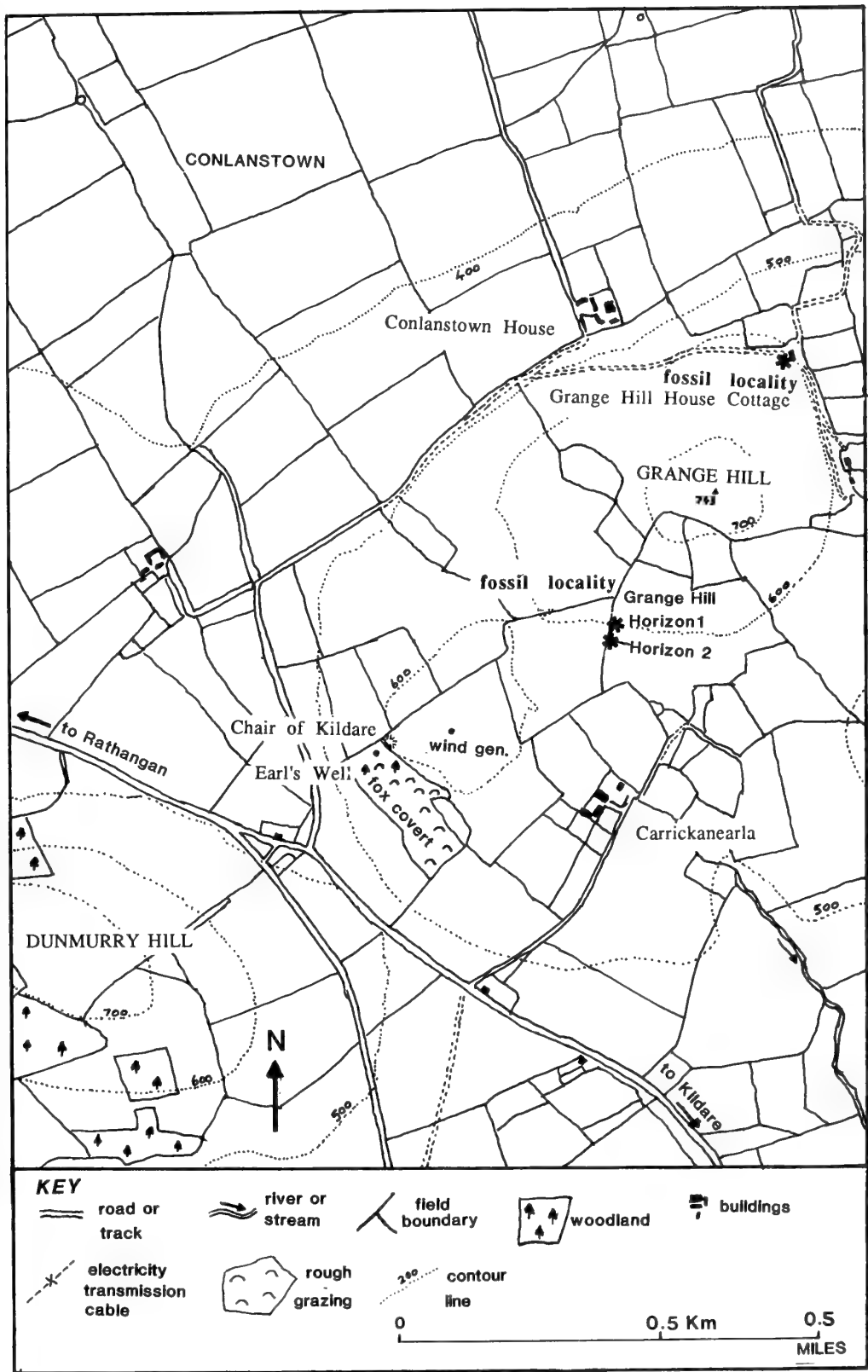
Fig. 2 Locality map of the three fossil localities in the Kildare inlier; Grange Hill House Cottage, Grange Hill Horizon 1 and Horizon 2.
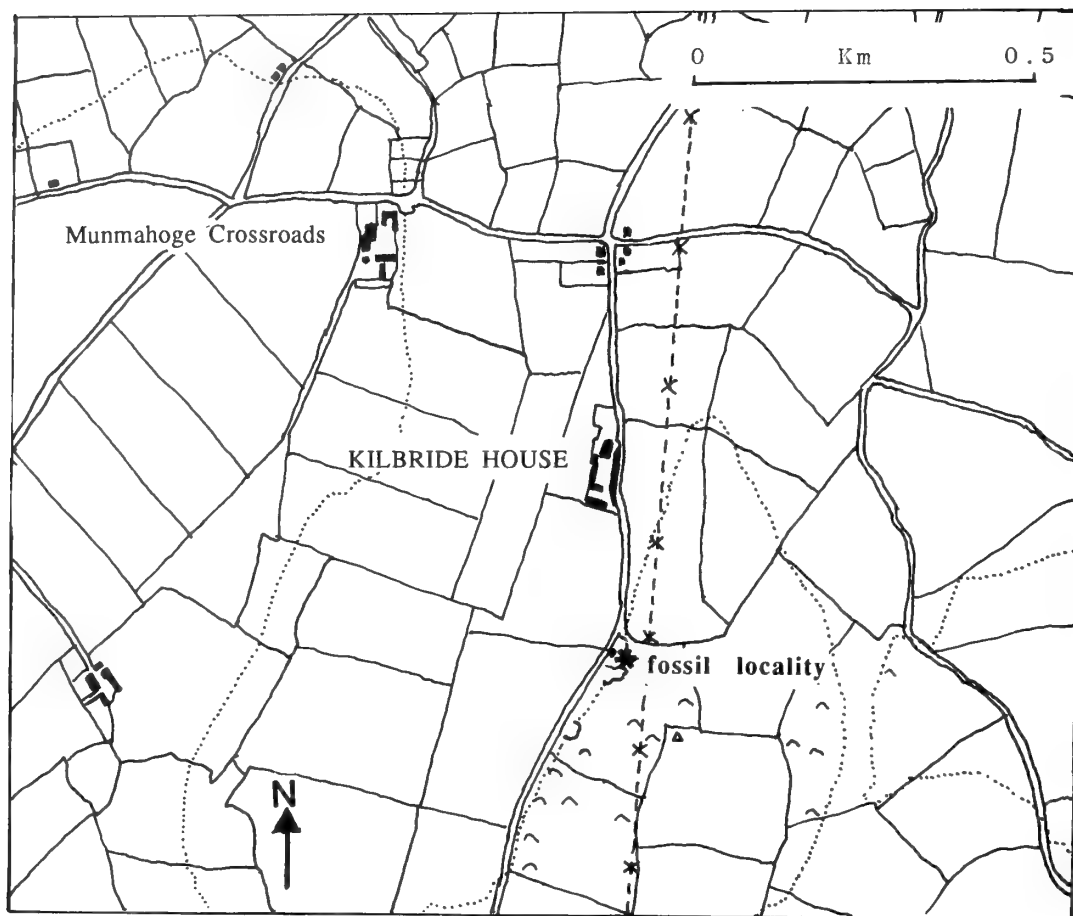
Fig. 3   Locality map of the Kilbride locality. Key as in Fig. 2.

any *in situ* exposure. However, collecting amongst loose blocks in the steep wooded slope within a restricted area yielded a large fauna comparable with that listed by Baily (*in* Hardman 1887). The fossils were found most frequently in blocks of tuff but others came from slaty siltstones and mudstones. The preservation is generally poor and identification proved difficult beyond generic level. The similarity of the fauna and lithology to that described in the memoir, and the limited section of slope where fossiliferous blocks were found, suggest that they are from the outcrop below the surface drift.

Carrigadaggan, Co. Wexford (1:126720 – SHEET 23, S313240)

Despite being one of the most fossiliferous localities in the Duncannon Group this site has received scant attention in the last 100 years. Its exact position is shown on Fig. 7. M'Coy (1846) gives this locality for many of his species – an impressive list of 16, mainly brachiopods and trilobites, but including the rhombiferan cystoid *Echinosphaerites granulatus* as an 'extremely common' element of the fauna. The faunal list given in the G.S.I. memoir (Kinahan 1879) is even more comprehensive. Thirty-eight genera are listed, again mainly brachiopods and trilobites but also several bivalve and gastropod species, as well as bryozoans, orthocones, conu-

lariids and *Echinosphaerites aurantium* (as a very abundant species). Forbes (1848) also dealt with the locality in connection with *Echinosphaerites*. Kelly (1860) included the locality in his Wexford list and, unusually, named some species found there. Paul (1973) mentioned it, as one of 14 major cystoid localities, although no details were given. Williams *et al.* (1972:57) noted the place as a shelly locality in the Caradoc rocks of Wexford and Waterford.

Ballygarvan Bridge, Co. Wexford (1:126720 – SHEET 23, S792188)

As one of the few fossil localities in south Wexford, Ballygarvan Bridge is often mentioned in connection with Carrigadaggan, but similarly until now no systematic re-collection of the faunas has been attempted since the late 19th century. M'Coy (1846) listed 9 species; the G.S.I. memoir (Kinahan 1879) has an increased diversity of 11, but with some different species. The exact locality from which previous collections were made is in some doubt. Although the description in the memoir is characteristically imprecise, the G.S.I. 6″ field-sheets have a precisely located asterisk indicating the locality. However, the geological boundaries adjacent to the bridge itself are complex and unclear, and since there is no exposure at the indicated spot the possibility of a cartographer's mistake must be kept in mind. The present exposure is very
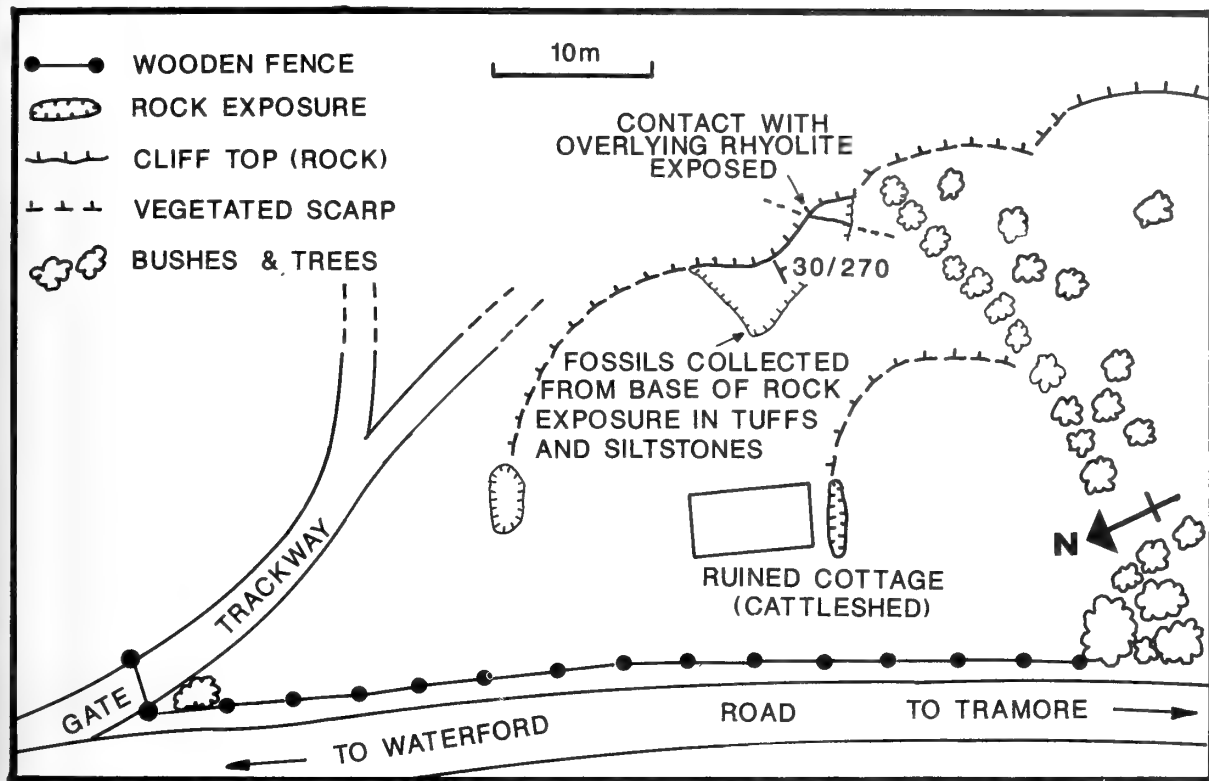
Fig. 4 Detailed plan of the Kilbride locality.

limited, but a collection was made from hard grey slates in the wooded banks of the river (see Fig. 8), approximately 20m away along the strike from the supposed locality. The fauna is sparse, although M'Coy (1846) described most elements of his list as common. All three collections were probably made from slightly different horizons in close proximity.

Frankfort and Clogh, Co. Wexford (1:126720 – SHEET 19, T109550 (Frankfort), T123555 (Clough))

These are listed by Baily (*in* Hardman 1887) as one locality. In fact the 1″ sheet 149 and the G.S.I. 6″ fieldsheets show three separate localities, all of which were investigated in the present work. No fossiliferous exposure was found at any site, although a few fossils were found in loose blocks at Clogh. The localities are the main source of fossils used to date the Ballymoney Formation of Hiller (1971) and Mitchell *et al.* (1972), although Hiller was only able to find wall blocks of fossiliferous rock, the original G.S.I. localities being infilled or overgrown. The localities are shown in Fig. 9.

Raheen, Co. Wexford (1:126720 – SHEET 23, S891326)

The original G.S.I. locality listed by Baily (*in* Kinahan 1882) for 1″ Sheet 158 is an old quarry now extremely overgrown, with almost no exposure. Fortunately, during this study the local farmer had excavated a new pit roughly along the strike about 5m away from the old pit, for hardcore. On my discovery, it was already half filled with domestic refuse and

is probably by now completely filled. This temporary exposure allowed collection of a large fauna. Fig. 10 shows the exact position of Raheen. The locality was not known to M'Coy (1846) or Kelly (1860), and after collection by the G.S.I. no attention was paid to it until the 1970s. Shannon (1979a: 46) recorded a fossil assemblage indicative of a Caradoc age. Brenchley *et al.* (1977) mentioned it in connection with specimens of *Plaesiomys,* presumably from existing collections. It is an important locality, therefore, in that it provides data along strike from better-known sections at Enniscorthy, and between there and Carrigadaggan to the southwest. It is also important in that the newly collected fauna differs somewhat from previously listed assemblages.

Greenville, Enniscorthy, Co. Wexford (1:126720 – SHEET 23, S962412)

This locality is the most important of several known from the environs of Enniscorthy. M'Coy (1846) listed many species from here, as did the G.S.I. memoir (Kinahan 1882 – locality 5). The locality was reviewed in detail by Brenchley *et al.* (1977), but it was revisited in this study, new material being collected for the sake of completeness, and with the specific aim of comparing elements of the brachiopod fauna with other sampled localities. It was also hoped to collect topotypic material of the poorly known agnostid trilobite *Trinodus agnostiformis* M'Coy, the type specimen of which was redescribed by Whittington (1950: 533). The site location is shown in Fig. 11. The rock is a very fractured buff coloured mudstone, occasionally tuffaceous. New material was excavated from shallow depth in the old farmyard, between the
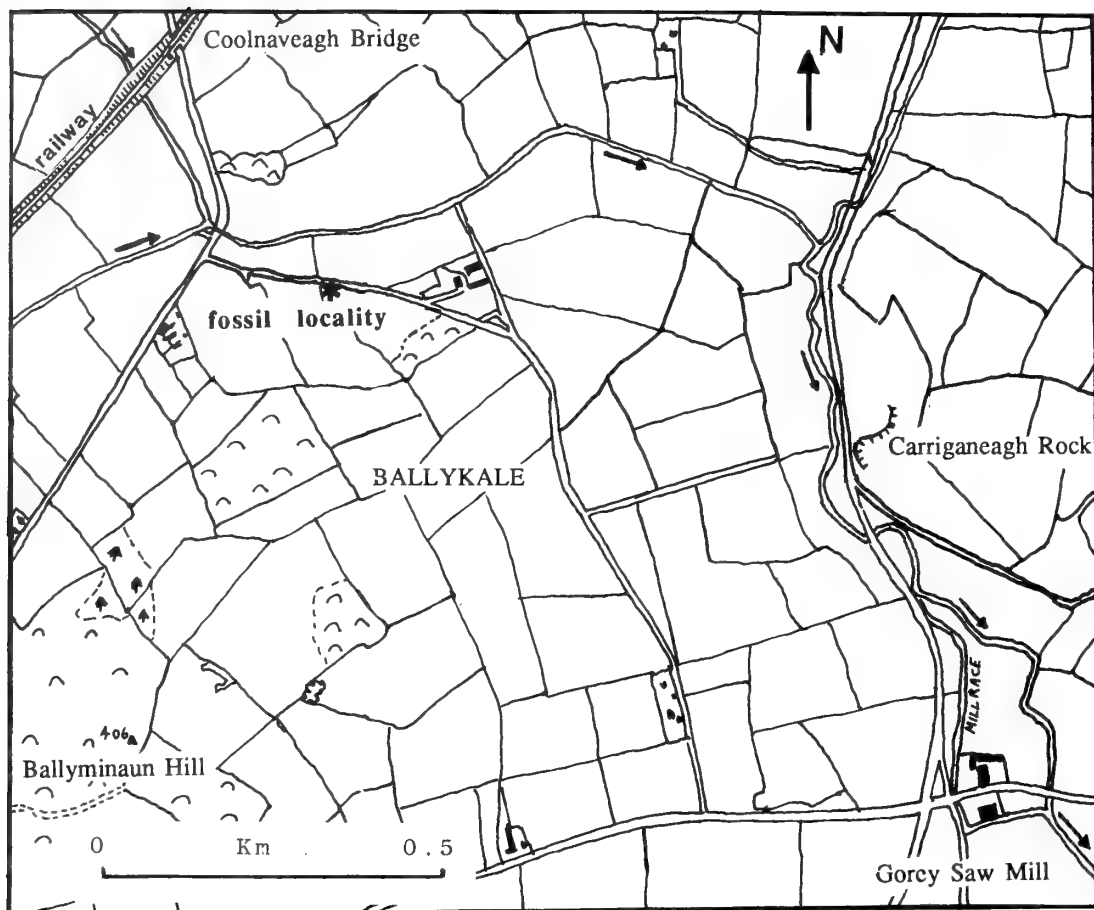
Fig. 5   Locality map of the Ballykale locality. Key as in Fig. 2.

lowest doorway of the ruined farmhouse and the new gateway to the northwest.

Greenville and Moyne Upper Boundary, Enniscorthy, Co. Wexford (1:126720 – SHEET 23, S967420)

This locality (Fig. 11) should not be confused with Greenville itself. G.S.I. locality 4 in Kinahan (1882) is Greenville and Moyne Upper Boundary, where a fauna was re-collected from many large blocks exposed as a result of very recent ploughing. These were immediately adjacent to the hedge bounding the original locality, an old quarry now slurry filled. No fossiliferous horizon was located within the exposure in the mainly volcanic quarry.

Courtown localities, Co. Wexford (1:126720 – SHEET 19, T187566 (Ballinatray)

Numerous localities in the area of Courtown are listed in an earlier section, Table 1 (p.110). These were reviewed by Crimes & Crossley (1968), Brenchley & Treagus (1970) and Mitchell *et al.* (1972). Further examination of all these localities failed, with one exception, to yield anything new or significant; fossils found were poorly preserved gastropods, a few external moulds of *Glyptorthis* and crinoid ossicles from

the Courtown Formation. No new material was recovered from the Ballymoney Formation. The only exception was a collection made from calcareous slates in the Ballinatray Formation, about 160 m west of Ballinatray Bridge (Fig. 12). The present bridge is probably more recent than that named in the G.S.I. memoir (Hardman 1887), since the Courtown to Gorey road has been re-aligned since the 6″ mapping. There is considerable confusion about the exact position of localities in this area, since both the 1″ and 6″ G.S.I. maps have a profusion of fossil locality asterisks, not all of which can be related to the named localities in the G.S.I. memoir. However, both from the described position and from the fauna present it appears that this might be locality 14 of Hardman (1887), where '*Illaenus Bowmanni*', '*Leptaena sericea*' and '*Orthis calligramma*' were recorded in some abundance.

Slieveroe, Rathdrum, Co. Wicklow (1:126720 – SHEET 16, T211890)

This highly fossiliferous locality was known to Griffith's collectors (M'Coy 1846) and to the G.S.I. mapping team (Jukes & Du Noyer 1869). It was re-collected after excavation by Brenchley *et al.* (1977) and a mixed brachiopod-trilobite fauna recorded from there. Although it was re-collected by me, the combination of very strong deformation in the fragile slates and shortage of time meant that no
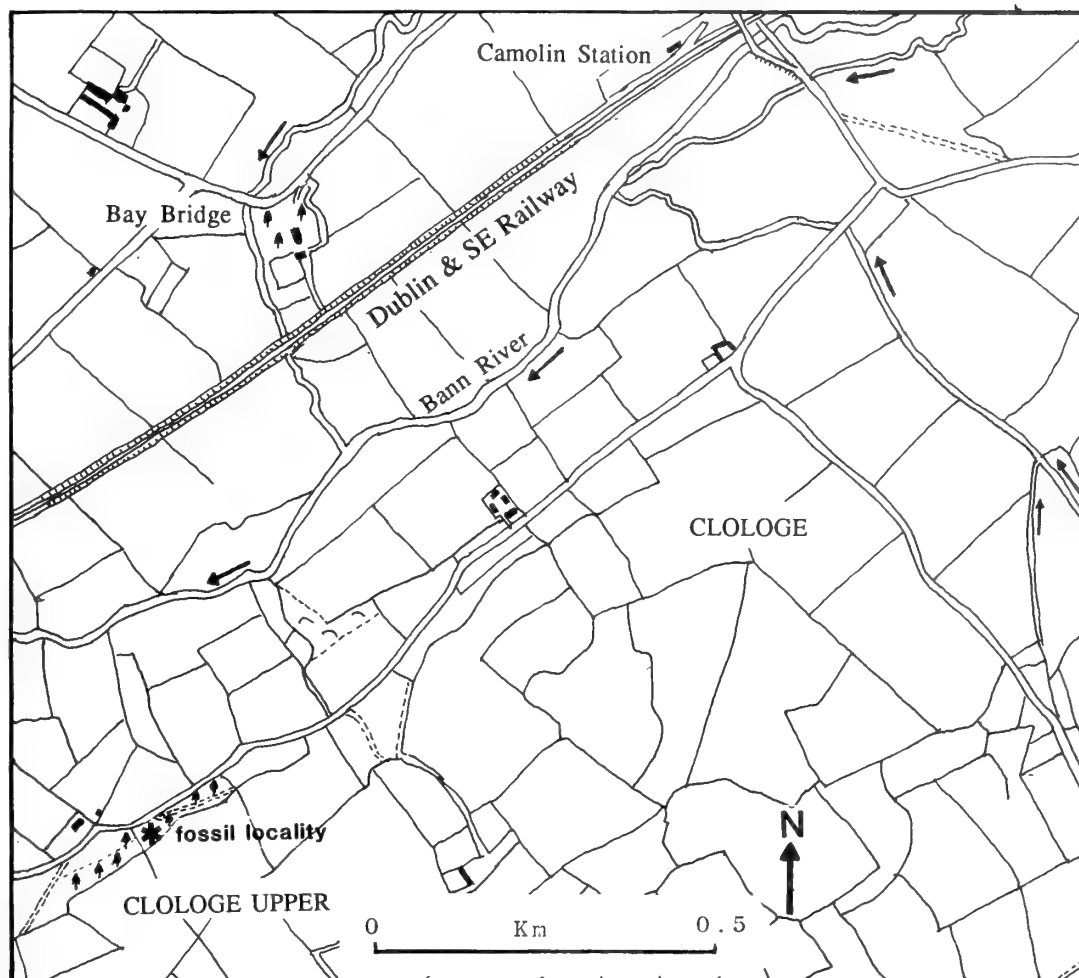
Fig. 6 Locality map of the Clologe Upper locality. Key as in Fig. 2.

further work was done on the material. The previous faunal lists are used in discussion of correlations.

Other localities

In the course of tracing the localities from the memoirs, several other records of fossils were noted. On Sheet 158 (Kinahan 1882: 26) a locality called Kellystown Bridge was described a little south of Raheen, but no details were given in the palaeontological notes and it was not traced on the G.S.I. 6″ fieldsheets nor in reconnaissance fieldwork. Kelly (1860) gave details of various localities which were not all included on the G.S.I. 6″ sheets or in the memoirs, including Ballyminaun Hill and Carriganeagh, both south of Gorey. These do not now have any fossiliferous exposure. Fossils were recorded by Shannon (1979a) from Raheen and Ballybrennan, both G.S.I. localities, and also from Wilton Castle southwest of Enniscorthy, but the area is now heavily forested and no fossils were found in the restricted exposure available. All other sites examined as a result of personal communications, or unnamed sites indicated by asterisks on 1″ and 6″ geological maps, proved to be either unfossiliferous or not now exposed.

METHODOLOGY AND TECHNIQUES

Sampling methods

In all sampled localities, an initial collection was made by identification of the fossiliferous lithology and on-site collection of specimens. Subsequently, the main collection of specimens was achieved by removing large volumes (between 10 kg and 80 kg, occasionally more) of the fossiliferous lithology, to be broken up and examined in a laboratory. The validity of this method was verified by the fact that successive seasons' collections served to increase the numbers of specimens, but not the diversity of the fauna. The one exception to this was the Kilbride locality near Tramore, Co. Waterford (p.112). This debris flow appears to have 'sampled' various benthic associations in its downslope movement, and subsequent collections made here increased the diversity of the fauna significantly from the initial sampling.
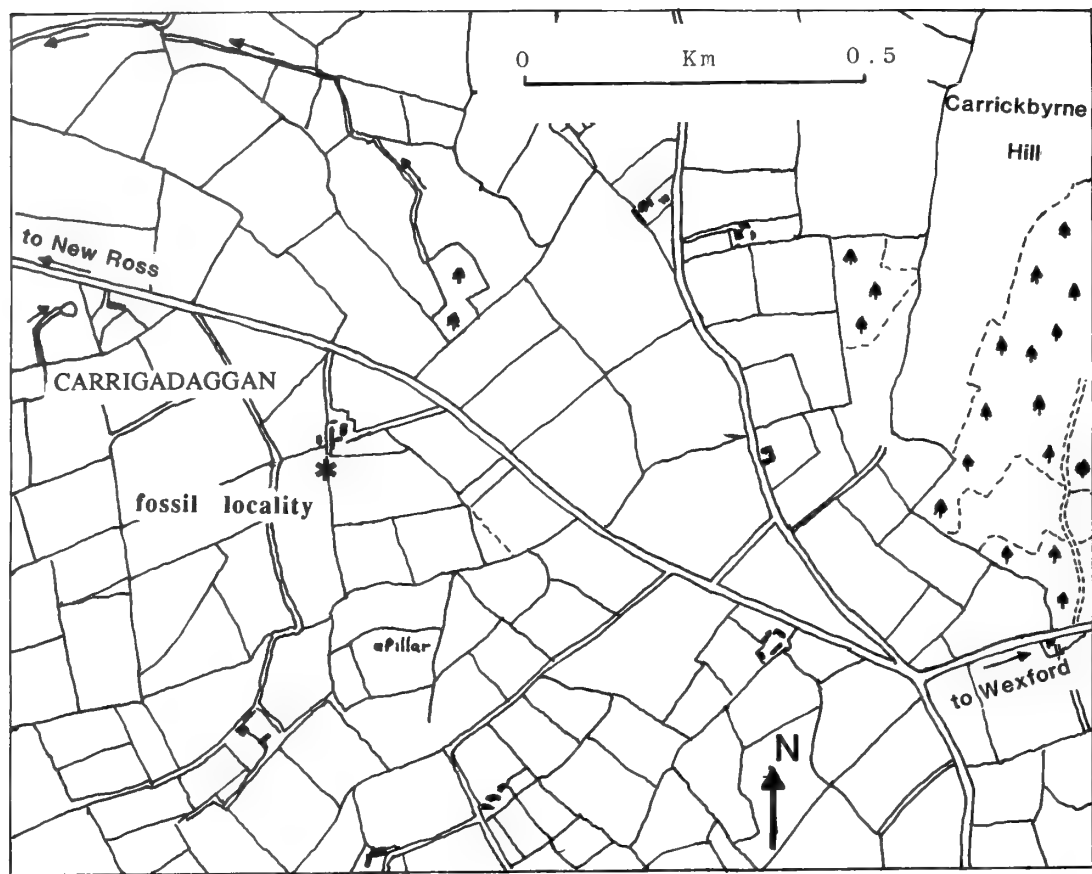
Fig. 7   Locality map of the Carrigadaggan locality. Key as in Fig. 2.

Preparation techniques

Standard preparation methods were used. The measurements of all material (in millimetres) were made using vernier scale calipers or a micrometric graduated microscope eyepiece, both accurate to 0·1 mm. The combination of camera, lenses and extension rings (Table 5) gave a range of magnifications of up to X5. The specimens were whitened with ammonium chloride sublimate before being photographed.

Taxonomy and statistical analysis

In this study both multivariate and bivariate analyses have been utilized where the measurement data were adequate.

Table 5   Magnifications obtained by different lens and extension ring combinations.

AF Micro-Nikkor 55 mm f/28	×1
AF Micro-Nikkor 55 mm f/2·8, PK11A, PK12, PK13	×2
24 mm lens reversed + PK11A	×3
24 mm lens reversed + PK13	×4
24 mm lens reversed + PK11A + PK12 + PK13	×5

NOTE: All other combinations produce non-integer magnifications. Magnification less than X1 necessitated the use of the AF Micro Nikkor 55 mm, but not fully extended. The magnification was calculated by comparison of the negative with the measured specimen size.

For detailed discussion of statistical methodology in brachiopod systematic work, reference can be made to Williams (1962), Harper (1984) and Temple (1987). In many older palaeontological references the use of statistics to define species is minimal or non-existent. For example, the fundamental work of M'Coy (1846) quotes the length of most species described as a single value (in inches and lines, where a line = $1/12^{th}$ of an inch). No indication is given as to whether this is the length of a figured specimen or a subjective assessment of the mean length of a sample. Here a pragmatic approach was taken, and measurements were made on any specimens worth measuring. Some measurements taken on slightly deformed material are included in descriptions in the text as a guide to proportions, but where this occurs it is pointed out. Table 6 is a set of defined variates as used by Harper (1984) and adhered to in the present work. Although in some cases the measurements taken did not provide sufficient reason to classify a sample as belonging to a particular species, the original data for these and all measured specimens is lodged in the General Library Biological Data Collection at The Natural History Museum, South Kensington, London. The figured specimens themselves are deposited in the Palaeontology Department collections there, register number prefix BC. Another set of the data is lodged in the James Mitchell Museum, University College, Galway, where all non-figured brachiopods and other material are deposited. Analysis was done using the 'Palstat' package on BBC microcomputers (Harper & Ryan 1987).
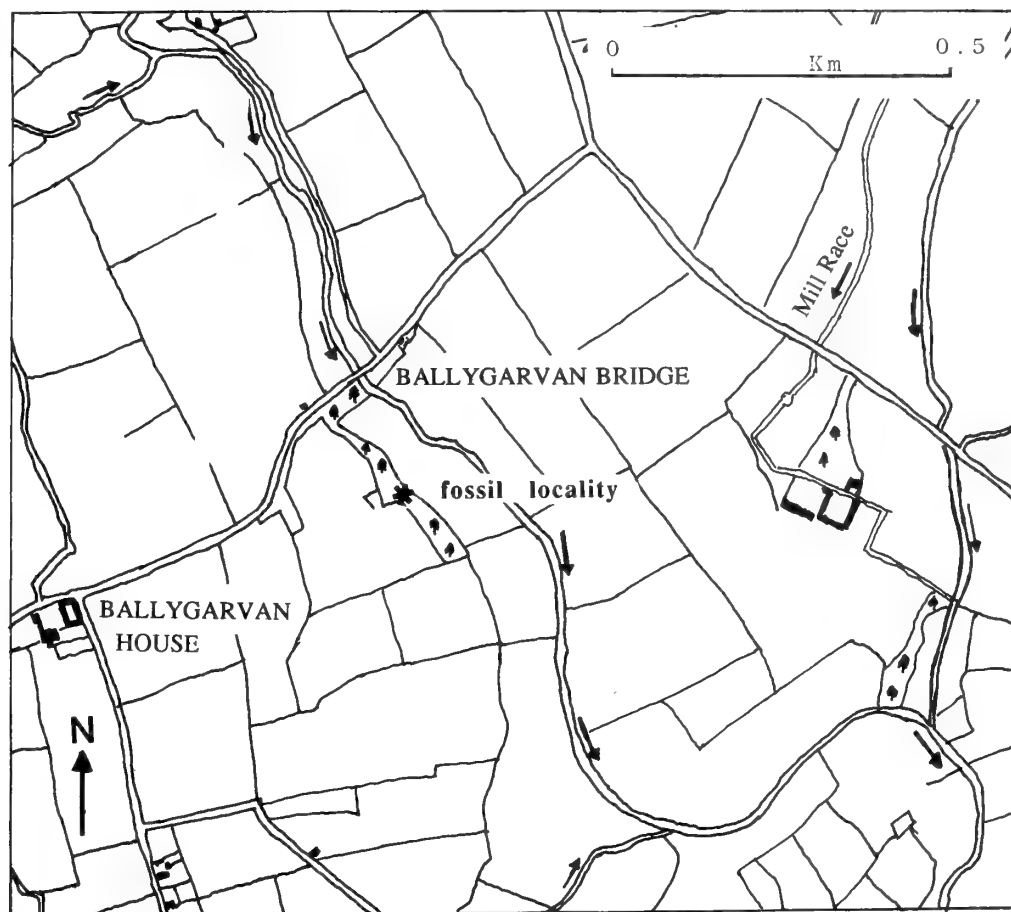
Fig. 8   Locality map of the Ballygarvan Bridge locality. Key as in Fig. 2.

STRATIGRAPHICAL CORRELATION

The stratigraphy of SE Ireland, as presently understood, is the result of many years work by innumerable individuals. The present study is concerned only with one part of the succession – the Duncannon Group, which is a mid-Upper Ordovician (mainly Caradoc) volcanic-dominated sequence, with clastic sedimentary intercalations. It is generally unconformable on the Lower Ordovician (Arenig – Llanvirn/ Llandeilo?) Ribband Group.

In certain better-exposed areas, notably Courtown (Brenchley & Treagus 1970, Mitchell et al. 1972) and Tramore (Stillman 1976, Carlisle 1979), more detailed stratigraphies have been erected with several local formations. The two areas of Courtown and Tramore were correlated on the basis of faunas and comparable stratigraphies by Mitchell et al. (1972), and the age subsequently revised by Carlisle (1979) through better knowledge of the extent of the gracilis Zone. Thus both the lowest calcareous horizons, the Tramore Limestone Formation and the Courtown Formation, are considered as late Llandeilo in age, or even older (Llanvirn- -Llandeilo) based on conodonts (Bergström 1971).

The thick development of volcanics west of Tramore and Waterford is perhaps the most complex area of the Duncannon Group and there is much debate as to the true sequence

there. Tietzsch–Tyler (1989) reviews the various arguments and draws his own interpretations for the G.S.I. compilation maps used in Parkes (1990). Stillman (1976) has noted that the succession is subdivided on lithostratigraphical grounds and should be regarded as comprising 'volcanogenic units', essentially derived from a volcanic centre situated about 4 km northwest of Tramore, and another farther west. The importance of fossil assemblages to date horizons within such sequences is thus clear, to confirm and supplement the petrological and field relationships of the units. The Tramore Limestone Formation and some gracilis-bearing shales were the only well-dated horizons until Carlisle (1979) recorded a shelly assemblage from Kilbride, which is described herein (Table 11, p.129). The assemblage, near the top of the succession, provides some constraint on the date of cessation of volcanism in Waterford. Consequently, although the age of the Kilbride fauna is discussed below, the remainder of the sequence and its faunas underlying the Kilbride assemblage is outside the scope of this review, as previously noted.

Re-examination of the Courtown localities collected by Crimes & Crossley (1968), Hiller (1971), Brenchley & Treagus (1970) and Mitchell et al. (1972) yielded no significant new information and the formations erected by these authors and the existing age constraints described from the fossil assemblages are thus accepted here. The development of
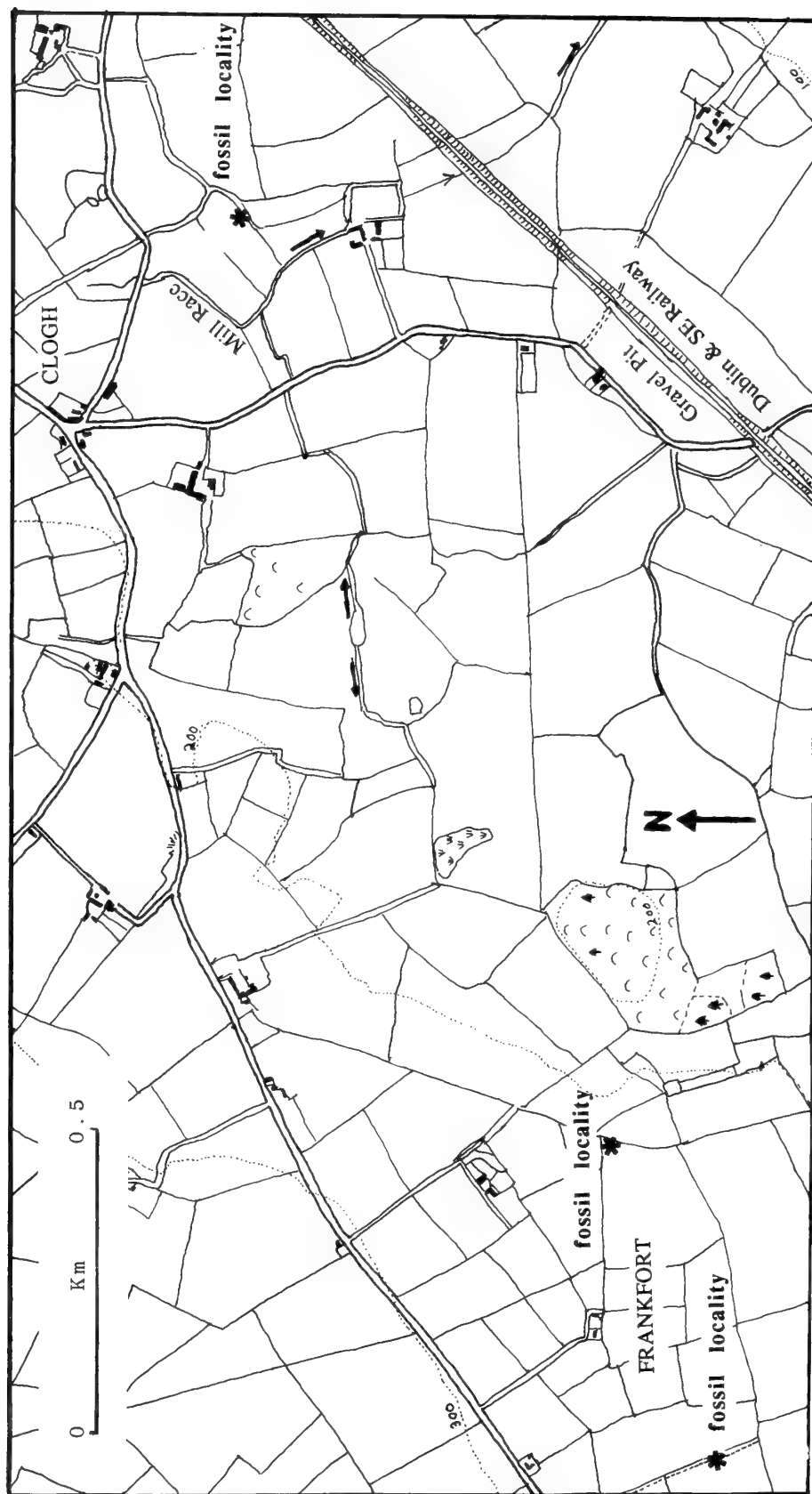
Fig. 9 Locality map of the Frankfort and Clogh localities. Key as in Fig. 2.
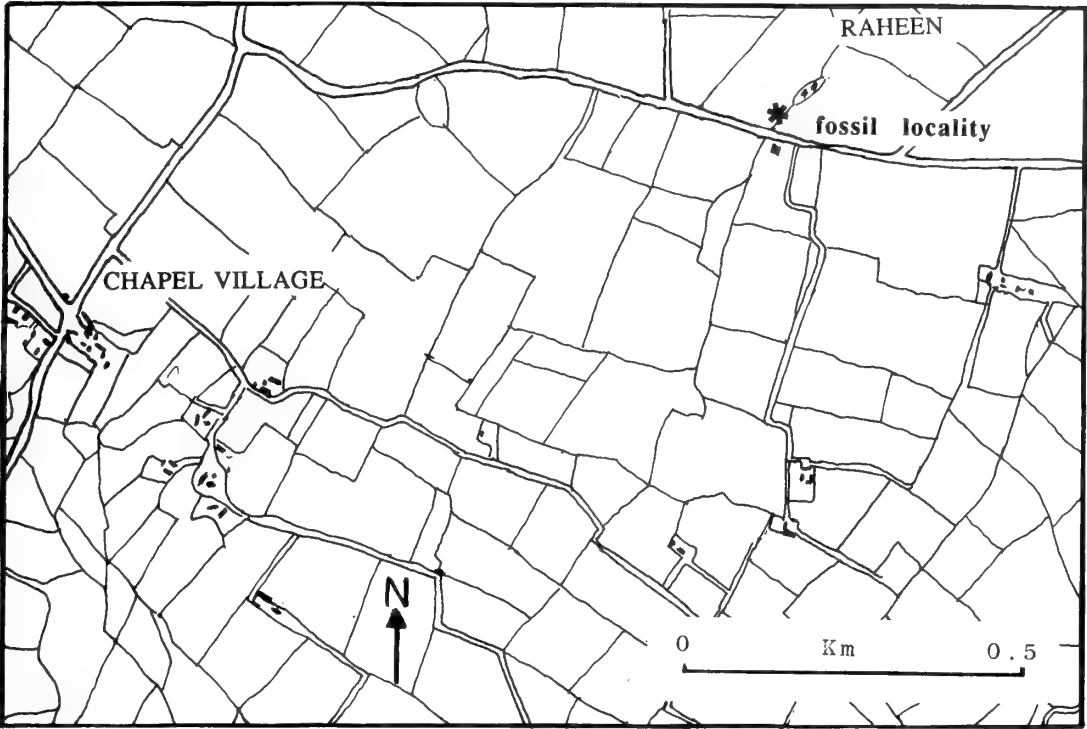
Fig. 10 Locality map of the Raheen locality. Key as in Fig. 2.

Table 6 Definition of variates measured on the fossil brachiopods in this paper.

X1	sagittal length
X2	maximum width
X3	position of maximum width measured from posterior margin
X4	maximum depth measured perpendicular to sagittal length
X5	hinge width
X6	maximum length of interarea
X7	origin of fold or sulcus measured from posterior sagittal margin
X8	maximum width of rim or limbus
X9	maximum length of muscle scar measured from posterior sagittal margin
X10	maximum width of muscle scar
X11	wavelength of median rib at 5 mm growth stage
X12	position of apex measured anteriorly from posterior margin
X13	length of base of spondylium
X14	maximum width of spondylium
X15	length of base of crurarium
X16	maximum width of crurarium
X17	anterior extension of brachiophore bases measured from umbo in plane of sagittal length
X18	transverse separation of ends in brachiophore bases
X19	maximum depth of sulcus
X20	maximum width of sulcus
X21	length of cardinal process base
X22	sagittal length of submedian septa
X23	transverse separation of anterior ends of submedian septa
X24	sagittal length of median septum

calcareous clastics followed by black graptolitic shales within *gracilis* times appears to have been restricted to the areas mentioned above, since no comparable sequence is recog-

nized elsewhere in the Duncannon Group, and has not been found in boreholes.

In between these two areas, the main belt of Duncannon Group rocks is poorly exposed, often as resistant hills of rhyolitic intrusions or thicker volcanic units which were probably original volcanic centres. The succession is poorly differentiated, despite several intensive studies. The Duncannon Group was defined by Gardiner (1974) from the Duncannon district of southwest Wexford and divided into four formations; Duncannon Volcanic Formation, Arthurstown Formation, Ballyhack Formation and Campile Volcanic Formation, all of Caradoc age based on graptolite evidence, in the regional Campile Syncline (Gardiner 1970). However, Shannon (1978, 1979a), in mapping the area south of Enniscorthy, but not continuous with the area of Gardiner (1967), differentiated the succession into only two Formations: the Doonooney Formation (with the Ballybrennan Volcanic Member) and the younger Raheenahoon Volcanic Formation, which encompasses the main rhyolitic volcanism. Both Raheen and Carrigadaggan are within the latter formation in the area mapped by Shannon. The remapping of mid Co. Wexford (Geraghty 1989) north of Shannon's area has confirmed the threefold division into Cahore, Ribband and Duncannon Groups.

Despite the poor exposure and limited extent of the inlier at Kildare, the sedimentary succession is more varied and the palaeontological constraints on the age of different horizons is better understood, although there are many problems remaining. The Duncannon Group equivalents probably lie unconformably upon the older rocks below them. A Soudleyan fauna and a Longvillian fauna constrain the age of volcanism here, being found above and below the lavas of Grange Hill. There are Ashgill faunas in the Kildare Lime-
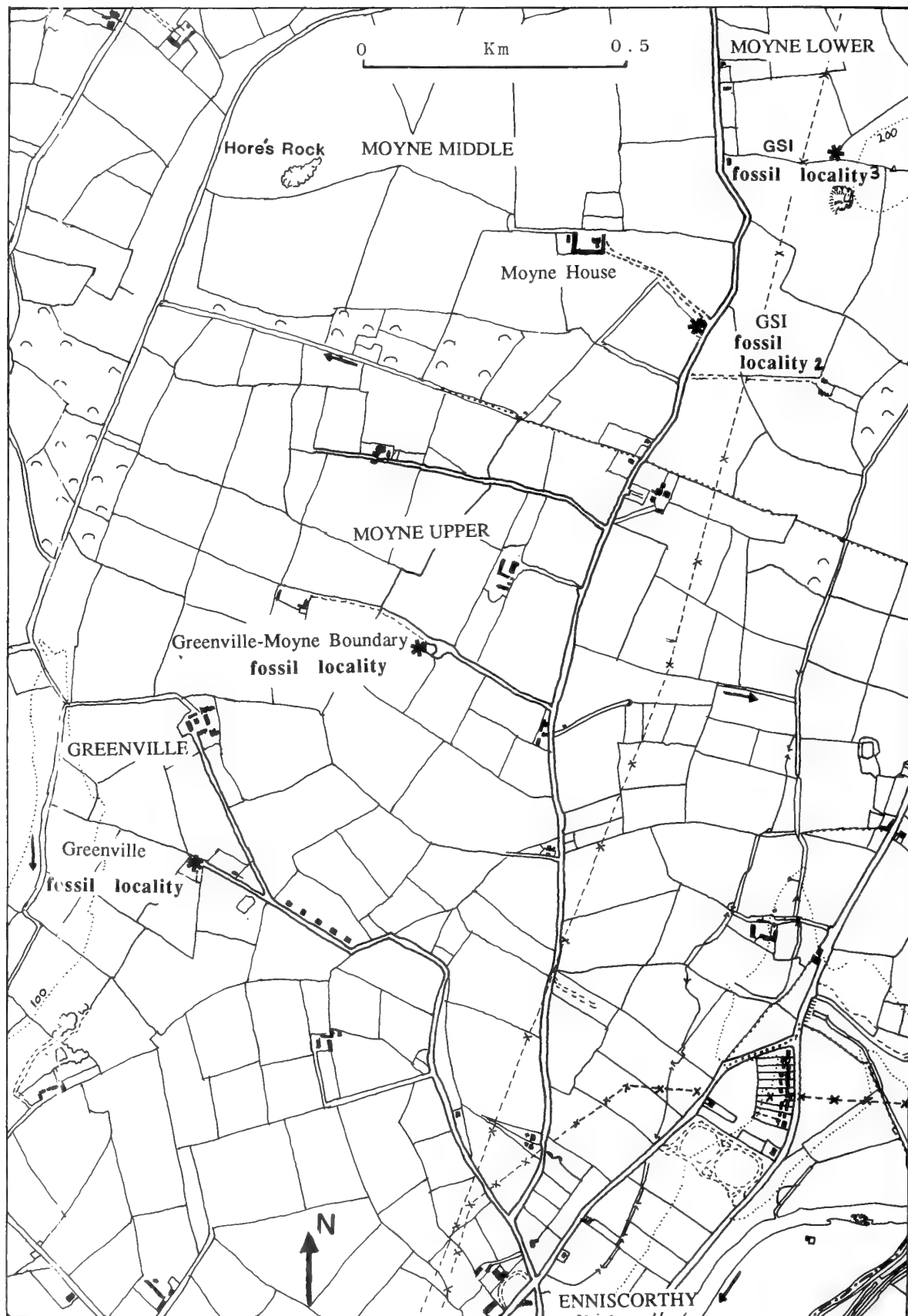
Fig. 11 Locality map of the Greenville and Greenville-Moyne Boundary localities and now unexposed G.S.I. localities at Enniscorthy. Key as in Fig. [?].
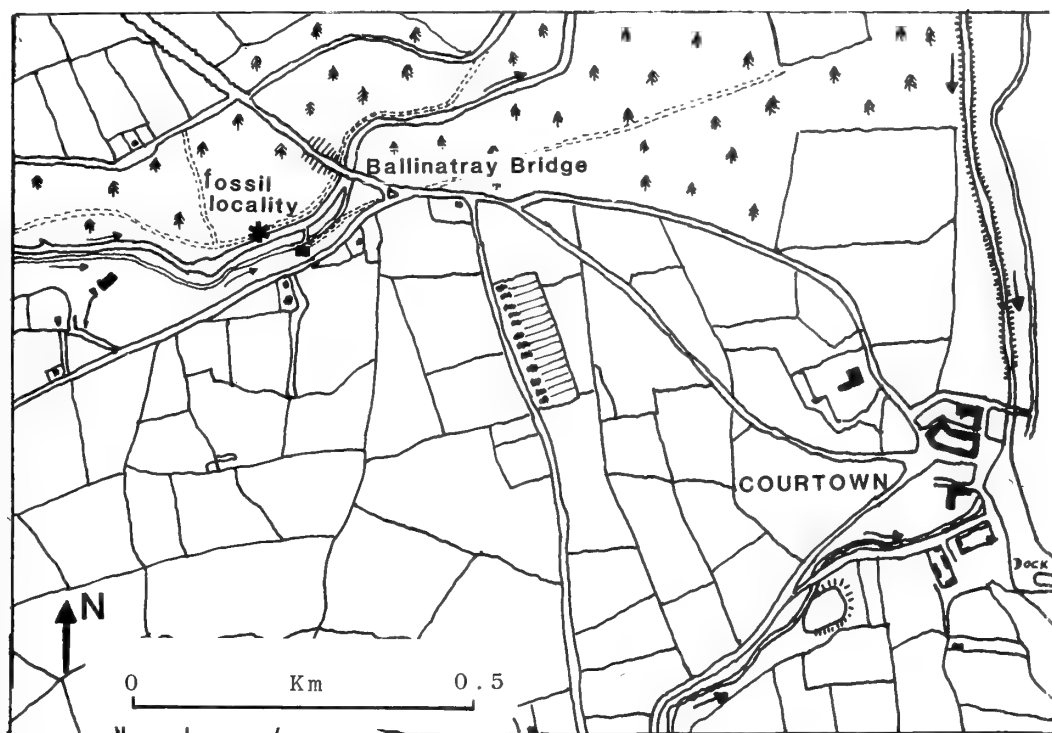
Fig. 12 Locality map of the Ballinatray locality. Key as in Fig. 2.

stone Formation (Rawtheyan) and the well known *Hirnantia* fauna in the topmost mudstones. A review of this inlier is given by Parkes & Palmer (1994). The stratigraphy of the eastern Ireland successions in the Iapetus suture zone has been investigated by Murphy (1987), who identified two separate terranes, the Grangegeeth and Bellewstown terranes, between the Balbriggan-Herbertstown sector of the Leinster terrane and the Central terrane (equivalent of the Southern Uplands of Scotland). These terranes are identified on the basis of contrasting volcanic characteristics and stratigraphical sequences as well as faunal differences. Murphy (1987) also correlated the sequences of eastern Ireland with those of the Leinster terrane and the Lake District of England.

Within the Leinster terrane, recent detailed reviews of the complete stratigraphical successions have been by Williams *et al.* (1972), Brück *et al.* (1978, 1979), and Holland (1981). More recently Harper & Parkes (1989) summarized the palaeontological constraints on the development of Irish Caledonide terranes, a subject expanded upon in Murphy *et al.* (1991). Parkes & Vaughan (1992) and Owen *et al.* (1992) have dealt specifically with the Grangegeeth terrane.

Tietzsch-Tyler (1989) has completed a re-evaluation of the Lower Palaeozoic geology, as well as the preparation of G.S.I. compilation maps, for south-east Ireland. This latter work involves numerous modifications which are outside the scope of the present work, but several redefined formations are used in the Duncannon Group, as explained in the key to those maps. Principal of these is the Annestown Formation, of essentially rhyolitic composition with andesite, slate and limestone members. This represents undifferentiated middle Duncannon Group sediments and volcanics on the map, and is the equivalent of the Doonooney and Raheenahoon Volca-

nic Formations of Shannon (1978). It is also equivalent to the Lower Tramore Volcanic Formation and all formations above (except the intrusive rhyolites in the Upper Tramore Volcanic Formation of Carlisle (1979)), the Duncannon, Arthurstown, Ballyhack and Campile formations of Gardiner (1974), and the Ballymoney and Gorey Rhyolite formations of Brenchley & Treagus (1970), as well as the Upper Caradoc Raheen Formation of Owen *et al.* (1986). Tietzsch-Tyler's Carrighalia Formation (equivalent to the Ross and Loftusacre Formations) with its Tramore Limestone Member is also the equivalent of the Courtown and Ballinatray formations of Brenchley & Treagus (1970).

AGE OF THE ASSEMBLAGES

Kildare, Grange Hill, Horizons 1 and 2

Wright (1970) claimed that these were Longvillian in age, on the grounds that their composition is similar to assemblages from the Gelli-grîn Formation of the Bala district of Wales, and in particular in relation to the presence of the calcareous inarticulate *Orthisocrania divaricata*, whose occurrence could only be substantiated in Longvillian rocks in Britain.

Whilst there are some differences noted (Tables 8, 9, p.128) between the assemblage described herein and that listed by Wright (1970), in essence the fauna still shows a strong affinity with the Welsh Bala faunas described by Williams (1963). Many of the genera are long-ranging in the Caradoc, or even the Ordovician, and where samples are inadequate to determine the species, then the overall generic composition has been used. However, at Grange Hill both

Orthisocrania divaricata and *Cremnorthis parva* occur, and these are at present only known from Longvillian rocks in Britain. *Leptestiina oepiki* is also recorded first in Longvillian Welsh localities (Williams 1963). Although *Cremnorthis* (Hints 1968, Llandeilo) and *Orthisocrania* (see p.136) are known from older Baltic successions and may have migrated to Leinster at a time different from their Welsh Basin arrival, on balance, with the total assemblage affinities with the Gelli-grîn Formation, a Longvillian age is most likely for this assemblage.

Given the close relationship of Grange Hill Horizon 2 to Horizon 1 with a substantially similar but reduced diversity assemblage, a similar Longvillian age is suggested for this horizon also. The position of the various localities at Kildare in the stratigraphical succession of the inlier is schematically illustrated in Fig. 13.

Kildare, Grange Hill House Cottage

The only modern reference to the faunal assemblage from this locality is Williams *et al.* (1972). A Soudleyan age is claimed for the fauna, presumably on the basis of comparisons with the faunal list published by Reynolds & Gardiner (1896). The recollection of the fauna, as described herein, confirms that suggested age. The palaeoecology of this assemblage differs substantially from other Duncannon Group faunas described here (Table 10, p.129), but the brachiopod species show a strong similarity with a fauna from Herbertstown, in the northernmost part of the Leinster

terrane, described by Harper *et al.* (1985). The combination of *Plaesiomys multiplicata* and *Oanduporella* cf. *reticulata* is unknown elsewhere in the Leinster terrane (except possibly at Clologe Upper). Indeed, the enteletoidean *Oanduporella* was unknown outside the Baltic before the Herbertstown record. The assemblage at Herbertstown was noted as being unlike any other fauna recorded in eastern Ireland (Harper *et al.* 1985: 289), but the new Kildare sample shows strong resemblances. On balance, the Herbertstown fauna was restricted to the Caradoc, with a most probable Soudleyan age. Similarly at Kildare, the fauna cannot be younger than Longvillian since it lies below the andesites of Grange Hill, which themselves are below a Longvillian assemblage. On the whole a Soudleyan age is most likely since the common brachiopod *Plaesiomys multiplicata* is found in the Soudleyan of Glyn Ceiriog of North Wales (Bancroft 1945) in association with *Rafinesquina*, which is present at Kildare too. The relationship of this horizon to others at Kildare is shown in Fig. 13.

Kilbride

At this locality Carlisle (1979) listed a fauna with some forms congeneric with those in the fauna described here (Table 11, p.129). There are several differences, but the principal genera are all indicative of a Caradoc age. Carlisle (1979: 552) recorded *Decordinaspis*, a trinucleid trilobite previously only found in the Harnagian/Soudleyan of Grangegeeth (Harper & Romano 1967). Thus she suggested a Soudleyan age for the base of the Upper Tramore Volcanic Formation, in which Kilbride is located, with an unknown upper limit but possibly extending into the Upper Caradoc. This author did not identify *Decordinaspis* here, but, based on the co-occurrence of *Cremnorthis parva*, *Leptestiina oepiki* and *Sowerbyella sericea*, a Longvillian age is postulated for the assemblage. This accords well with Carlisle's interpretation. If the *Orthisocrania* she recorded proves to be *O. divaricata*, this would further enhance the reliability of the age assigned, since the locality was said (Carlisle 1979: 551) to be 200 m above the base of the formation.

Ballykale

This assemblage is relatively low in both specimen numbers and diversity, being dominated by *Bimuria* cf. *dyfiensis* (81%, see Table 12, p.130). This species has only been described previously from the Gelli-grîn Formation of north Wales (Lockley 1980:215), which is of Longvillian age. In the other localities dealt with here, *Bimuria* sp. definitely occurs only at Kilbride, in a form probably conspecific or at least very close to *B.* cf. *dyfiensis*. This locality too is of probable Longvillian age and this seems the most reasonable estimate for the age of the Ballykale assemblage also. The few other brachiopods are all congeneric with Kilbride forms, notably the rare *Ptychoglyptus*.

Clologe Upper

Since the poor preservation of fossils from here permitted only a generic level identification at best, the precision of correlation can only be crude. Overall, the generic composition indicates a Caradoc age and some strong similarities with the other assemblages described herein. However, the possible occurrence of both *Oanduporella* and *Plaesiomys*, both
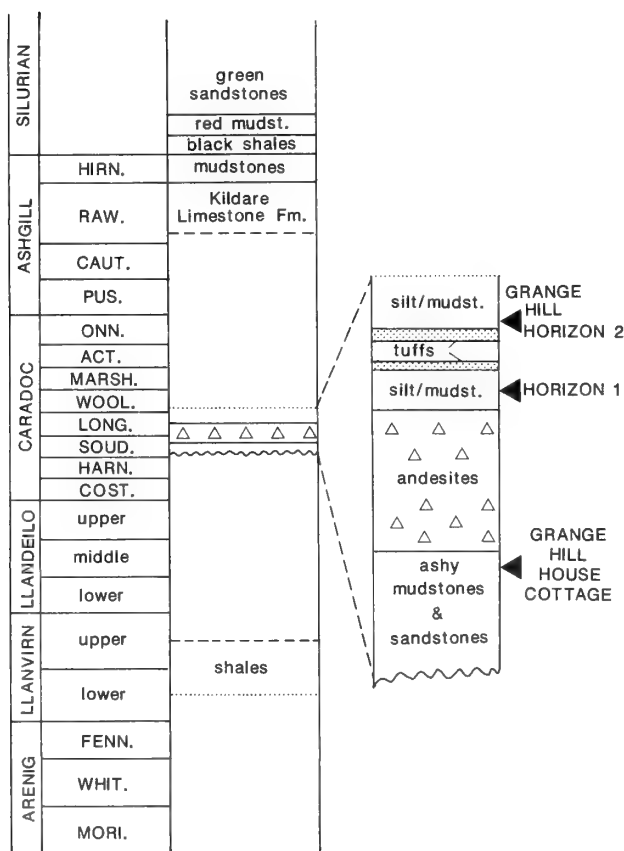
Fig. 13   Schematic section of the succession in the Kildare inlier.

reminiscent of the Soudleyan fauna at Grange Hill House Cottage, Kildare and the Soudleyan Herbertstown assemblage (Harper *et al.* 1985), together with the apparent absence of *Cremnorthis* and *Orthisocrania,* suggest that the assemblage is older than Longvillian. Therefore, a probable Soudleyan, or perhaps Harnagian, age is postulated.

Carrigadaggan

The brachiopod fauna contains numerous elements which allow confident assignment of the assemblage to the Longvillian, and enhance the strong inter-locality correlation. *Leptestiina oepiki, Cremnorthis parva, Orthisocrania divaricata, Sowerbyella sericea, Skenidioides costatus* and *Kullervo* aff. *hibernica* are all found in the Longvillian of Grange Hill, Kildare, as are many of the genera such as *Nicolella, Platystrophia* and *'Orthambonites'.* The species listed above, except *Orthisocrania* and *Kullervo,* are here recorded at Kilbride also (Table 14, p.131); Carlisle (1979) also listed *Orthisocrania* from there. The presence of *Saukrodictya* sp. is noted here, which although rare, also occurs at Kilbride, Ballykale and Greenville-Moyne, all of which are probably of Longvillian age. The cystoid *Echinosphaerites* cf. *granulatus* is most common here, but was also found at Kilbride and Ballygarvan Bridge. Although not stratigraphically useful, its occurrence in these three geographically close localities is supportive of the brachiopod correlation.

Ballygarvan Bridge

The sparse brachiopods from this locality allow little certainty about correlation of the assemblage, neither does the restricted trilobite material. The generic composition and abundance of gastropods (Table 15, p.131) is notably similar to that of Grange Hill (Table 8, p.128) and Grange Hill House Cottage (Table 9, p.128) at Kildare. This may be merely ecological control. However, as the large inarticulate *Lingulella ovata* occurs elsewhere in Leinster only in the Longvillian of Grange Hill, Kildare, a possible Longvillian age is suggested. In spite of the low numbers of specimens, the congeneric forms enhance the consistency of inter-locality correlation in the Duncannon Group.

Frankfort and Clogh

The examination of these localities was unproductive for new assemblages. However, the collections made by N. Hiller (for a B.Sc. thesis, 1971) and subsequent publication (Mitchell *et al.* 1972) correlating the Courtown area with the Tramore region, and now housed in the Ulster Museum in Belfast, were examined for comparison with other collections made in the present study. The list of genera published by Mitchell *et al.* (1972) is quite long but does not reflect the proportions within the assemblage. The strong deformation and poor preservation in the tuffaceous rocks, collected from walls in the area of the G.S.I. locality, made unequivocal identifications difficult. Many genera are represented by one questionable specimen only. The abundant genera are *Cremnorthis, 'Orthambonites', Leptestiina* and dalmanelloids. Less common but positively present are *Kullervo, Platystrophia, Anisopleurella, Skenidioides, Nicolella* and *Orthisocrania.* The apparent absence of some of the other listed genera could be due to incomplete donation of the collection, rather than absence from the assemblage, since not all specimens

were clearly labelled. The particular elements not seen in the material at the Ulster Museum were *Diambonia, Ptychoglyptus, Eoplectodonta, Pseudolingula* and *Actinomena?* The *Christiania* recorded is a somewhat equivocal single specimen which is highly strained.

Thus, if the definitely present and abundant elements alone are considered, the assemblage clearly takes on a strong resemblance to the described assemblages from Grange Hill, Carrigadaggan, Greenville-Moyne and other localities in Wexford. The re-examination of this assemblage, in conjunction with a revision of the Duncannon Group localities throughout Wexford and elsewhere in the Leinster terrane, reinforces the Upper Soudleyan – Longvillian age assigned to the Ballymoney Formation by Carlisle (1979: 552; fig. 3). On the basis of the existing brachiopod collections this will not be refined further, but new material or the current examination of the trilobite collections in the G.S.I. may yield better information.

Raheen

The assemblage described here (Table 16, p.131) is clearly inadequate for a confident correlation and is probably facies controlled, rather than of different age from other localities in the Duncannon Group. When the trilobite identification is complete a better constraint on the age might be made, but in the absence of better material the G.S.I. lists (Kinahan 1882) give a good indication of the age of adjacent beds in the succession. There are no species known to be restricted temporally, but typical Longvillian genera are absent. Some elements are reminiscent both of Greenville and the Brickworks Quarry Shale Formation of Grangegeeth (Romano 1980a), which are believed to be Harnagian or Soudleyan. Therefore, an early Caradoc age, possibly Harnagian or Soudleyan, is thought to be the best estimate.

Greenville

The collections made here (Table 17, p.132) are somewhat reduced by comparison with those of Brenchley *et al.* (1977). These authors suggested a Harnagian age, and no significant evidence has been found to dispute that in the assemblage described here. Only the probable occurrence of *Oanduporella,* present in the Soudleyan of Herbertstown (Harper *et al.* 1985) and in the Soudleyan assemblage at Grange Hill House Cottage, Kildare, suggests a possible Soudleyan age. Brenchley *et al.* (1977) attached some significance to the presence of 'an early species of *Sericoidea* together with *Anisopleurella* aff. *multiseptata* Williams'. As discussed in the systematic description of *Chonetoidea* (the senior synonym of *Sericoidea*), the variation amongst the population is considerable and assignment to *C.* aff. *abdita* Williams would now only suggest a Lower Caradoc age. *Anisopleurella multiseptata,* described from the Costonian Derfel Limestone Formation (Whittington & Williams 1955), is known also from the Longvillian Gelli-grîn Formation of Bala, North Wales (Lockley 1980).

Greenville-Moyne

Several elements, such as *Cremnorthis parva, Leptestiina oepiki* and *Skenidioides costatus,* are conspecific with samples from Longvillian assemblages at Kilbride, Carrigadaggan and Grange Hill Horizon 1 at Kildare. Other forms only identifi-

Fig. 14 Stratigraphical correlation chart for selected localities within the Leinster terrane of SE Ireland. *Sources*: Lambay/Portrane: various including Williams *et al*. 1972. Murphy 1987. Balbriggan: Murphy 1987. Rathdrum/SE Wicklow: Brück *et al*. 1979. Kildare: Williams *et al*. 1972, this study. Courtown: Carlisle 1979, Brenchley & Treagus 1970. Greenville/Enniscorthy: Brenchley & Treagus 1970, this study. Carrigadaggan/New Ross Area: this study, Tietzsch-Tyler 1989. Duncannon: Carlisle 1979. Kilbride/Tramore: this study.

able generically or questionably assigned, e.g. *Nicolella* sp., '*Orthambonites*' sp., *Orthisocrania*?, *Rhactorthis*? and *Sowerbyella*?, are all reminiscent of those assemblages, as is the rare occurrence of *Saukrodictya* sp. *Kullervo* aff. *hibernica* is also present at Greenville-Moyne, Carrigadaggan and Grange Hill Horizon 1, all localities thought to be Longvillian in age, but it also occurs in the Knockerk House Sandstone Member (Romano 1980a) of the Grangegeeth Group (equivalent to the Upper Tuffs and Shales of Harper, 1952), which is believed to be Costonian in age (Brenchley et al. 1977). However, the consistency of the inter-locality correlations suggest that a Longvillian age is most probable for the Greenville-Moyne assemblage.

Ballinatray

Although the assemblage from here is too deformed and broken to identify the brachiopods precisely, the age of the horizon is constrained by previous work. The age of the older Courtown Limestone Formation is believed to be mainly Llandeilo ranging up to the Costonian Stage of the Caradoc on the correlation with the Tramore Limestone Formation (Carlisle 1979). The succeeding Ballymoney Formation is believed to be of probable Longvillian age, and in any case *gracilis* Biozone graptolites have been recovered from the Ballinatray Formation (Mitchell et al. 1972). An early Caradoc, at least partly Costonian age is suggested for the formation.

In the light of the age constraints clarified by a revision of these Duncannon Group faunas a revised correlation chart has been produced (Fig. 14), with sections additional to previously published correlations e.g. Williams et al. (1972) and Brück et al. (1979).

PALAEOECOLOGY AND BIOGEOGRAPHY

In some of the localities very little ecological data can be derived because the exposures were small, resricted and isolated from a clearly defined succession, or assemblages were not from *in situ* rocks. Equally, small assemblages like those from Ballygarvan Bridge (Table 15) are inadequate for detailed interpretation. Even with large assemblages such as Grange Hill Horizon 1 (N=646) some reservations are held about interpreting too much from them.

One evident point from this work is that assemblages often differ from previously recorded collections, especially those of M'Coy (1846) and the G.S.I. Memoirs. Many differences are simply taxonomic artefacts reflecting better systematic differentiation of this important phylum. Where the outstanding differences are not addressed directly below, the best explanation is that in the volcano-sedimentary setting of these localities the character of faunas changed as a result of tuff falls etc. and slightly different horizons have been sampled. This would apply to Ballygarvan Bridge, Raheen, Greenville and possibly Greenville-Moyne for example.

For each locality a table of the total collected fauna is presented. Table 7, however, is a summary chart of presence/absence data for each locality, highlighting the inter-locality affinities. The tables (8–19) include total counts of the brachiopod valves and various animals for the comparison of assemblages with recognised palaeocommunities discussed below. Following Lockley (1980: 171) this number has been

Table 7 Summary chart of fauna collected at each locality. Localities: A – Kildare, Grange Hill Horizon 1. B – Kildare, Grange Hill Horizon 2. C – Kildare, Grange Hill House Cottage. D – Kilbride. E – Ballykale. F – Cloghoe Upper. G – Carrigadaggan. H – Ballygarvan Bridge. I – Raheen. J – Greenville. K – Greenville-Moyne. L – Ballinatray.

	A	B	C	D	E	F	G	H	I	J	K	L
BRACHIOPODS												
Acanthocrania?	●	–	–	●	–	–	–	–	–	–	–	–
Anisopleurella cf. *multiseptata*	–	–	–	●	–	●	–	●	–	–	–	–
Bicuspina?	–	–	–	●	–	●	–	●	–	–	–	–
Bimuria cf. *dyfiensis*	–	–	–	●	–	●	–	–	–	●	●	–
Bimuria sp.	–	–	–	●	–	●	–	–	–	●	●	–
Chonetoidea abdita	●	–	–	●	–	–	–	●	●	–	●	–
Cremnorthis parva	●	–	–	●	–	–	●	–	–	–	●	–
dalmanellids indet.	●	●	●	●	●	●	●	●	–	●	●	●
Dolerothis?	–	–	–	●	–	●	–	–	●	●	–	●
Glyptorthis	–	–	–	●	–	●	●	–	–	●	●	–
Hedstroemina sp.	●	●	–	●	–	–	–	–	–	–	–	–
Hesperorthis sp.	–	–	–	●	–	●	–	–	–	–	●	–
Hibernodonta?	–	–	–	●	–	●	–	–	–	●	–	–
Kjaerina?	–	–	–	–	–	●	–	●	–	–	–	–
Kjerulfina?	●	–	–	–	–	–	–	–	–	–	–	–
Kullervo aff. *hibernica*	●	–	–	●	–	–	●	–	–	–	●	–
Leptaena sp.	●	●	●	–	●	–	–	–	–	–	–	–
Leptellina cf. *llandeiloensis*	–	–	–	–	–	–	–	–	–	–	–	–
Leptestiina oepiki	●	–	–	●	–	●	●	–	–	●	●	●
Leptestiina oepiki ampla	–	–	–	–	–	●	–	●	–	–	–	–
Lingulella ovata	●	●	–	●	–	–	●	●	–	–	●	–
Nicolella cf. *actoniae*	●	–	–	●	–	●	●	–	●	–	●	–
Oanduporella cf. *reticulata*	–	–	●	–	–	●	–	●	–	–	●	–
'*Orthambonites*' sp.	–	–	–	●	–	●	–	–	●	●	●	–
Orthisocrania divaricata	●	●	–	●	–	●	–	–	–	●	●	–
Oxoplecia?	–	–	–	–	–	●	–	–	–	–	●	–
Petrocrania harperi	●	●	●	–	–	–	–	–	–	–	–	–
Philhedra sp.	●	–	–	–	–	–	–	–	–	–	–	–
Plaesiomys multiplicata	–	–	●	–	●	–	●	–	–	–	●	–
Platystrophia sp.	●	●	●	●	●	●	●	–	–	–	●	–
Porambonites sp.	–	–	–	–	–	–	–	–	●	–	–	–
Ptychoglyptus sp.	–	–	●	–	●	–	●	–	–	–	●	–
Rafinesquina sp.	–	–	●	–	●	–	–	–	–	–	–	–
Rhactorthis sp.	●	–	–	–	–	–	–	–	–	●	●	–
Salopia sp.	–	●	–	●	–	●	●	●	–	–	●	–
Saukrodictya cf. sp. A	–	–	–	●	–	●	●	–	●	–	●	–
Schizotreta sp.	–	–	●	–	●	–	–	–	–	–	–	–
Skenidioides costatus	●	●	●	●	●	–	●	–	–	●	●	–
Sowerbyella sericea	●	●	●	●	●	–	●	●	–	●	●	●
Strophomena?	●	–	–	–	–	–	–	–	–	–	–	–
TRILOBITES												
Ampyx austinii	–	–	●	–	●	–	●	–	–	–	●	–
Arthrorhachis	–	–	●	–	●	–	–	–	–	–	●	–
Atractopyge	–	–	–	–	●	–	●	–	●	–	–	–
Autoloxolichas	●	–	–	–	–	–	–	–	–	–	–	–
Calyptaulax	●	–	●	–	●	–	●	–	–	–	●	–
Deacybele	–	–	–	–	–	–	●	–	●	–	–	–
Encrinuroides	–	–	–	–	–	–	–	–	–	–	–	●
Flexicalymene	●	–	●	–	–	–	–	–	–	–	–	–
Homalopteon sp.	–	–	–	–	–	–	–	–	–	●	●	–
Remopleurides	–	–	–	–	–	–	–	–	●	●	–	–
Tretaspis	–	–	–	–	●	–	●	●	–	–	●	–
'*Trinodus agnostiformis*'	–	–	–	–	●	–	●	–	–	–	●	–
Xylabion	–	–	●	–	●	–	–	–	–	–	–	–
OTHER ELEMENTS												
Echinosphaerites granulatus	–	–	●	–	●	–	●	●	–	–	●	–
cheirocrinid cystoid	–	–	–	–	–	–	●	–	–	●	●	–
crinoid ossicles	●	–	●	–	●	–	●	●	–	●	●	●
gastropods	●	●	●	–	●	–	●	●	●	–	●	–
ramose bryozoans	●	–	●	–	●	–	●	●	–	●	●	–
prasoporid bryozoans	●	●	●	–	●	–	●	●	–	–	●	–
tentaculitids	●	–	–	●	–	●	–	–	–	–	●	–
orthocones	●	–	●	●	●	–	●	●	–	–	●	–
bivalves	●	●	●	–	●	–	●	–	–	–	●	–
conulariids	●	–	–	●	–	●	–	●	–	●	●	–
ostracods	–	–	●	–	●	–	–	–	–	–	●	–

calculated using the formula:

$$N = A + 0.5I + P \text{ (if P>B), or } N = A + 0.5I + B \text{ (if B>P)}$$

where: A = no. of articulated valves, B = no. of brachial valves, P = no. of pedicle valves, I = no. of indeterminate valves.

The problems of counting different groups of animals was discussed by Lockley (1980: 171–2) for Welsh Caradoc faunal associations and by Jaannusson (1984) for Baltoscandian Ordovician sequences. In the case of groups other than brachiopods absolute numbers are given. However, for some organisms such as fragmentary bryozoans, cystoid plates and crinoid ossicles, absolute numbers are given in brackets and an equivalent number of individuals given, generally one. An arbitrary correction factor is applied to bivalves for Kildare Grange Hill House Cottage, by halving the total, on the assumption that the valves are simply disarticulated in equal proportions. This is also applied to ostracods. For trilobites the largest value of pygidia or cephala is arbitrarily taken as

the number of individuals. Since brachiopods are generally the commonest animals, errors involved in counting other animals are considered as negligible.

The diverse assemblage from Kildare Grange Hill Horizon 1 is listed in Table 8. All the material consists of moulds from decalcified mudstone/siltstone. The ratio of ventral to dorsal valves is generally equal. Differences may be accounted for by the problems of identifying fragments produced by the sampling method. There is a large range of size variation between and within species, and there is no suggestion of current winnowing. The shells are disseminated through the sediment, not collected together as in a coquina. For these reasons the assemblage is treated as a palaeocommunity. Grange Hill Horizon 2 (Table 9) is very similar but has reduced frequency of fossils and the addition of common *Lingulella ovata*. The difference is partly because the rock is not decalcified. This biased the identifications in favour of larger distinctive species such as *L. ovata*, *O. divaricata* and *Platystrophia*. Another factor is that at least one thin tuff horizon is found between the two horizons, which may have subtly changed the assemblage.

Some differences between Table 8 and the faunal list of Wright (1970) should be noted. *Cyclospira* and *Bicuspina* were not collected by me, whilst taxa not recorded by Wright but collected by me include *Acanthocrania?*, *Chonetoidea*, *Hedstroemina*, *Kjerulfina*, *Kullervo* aff. *hibernica*, *Leptestiina oepiki*, *Lingulella ovata*, *Nicolella* cf. *actoniae*, *Petrocrania harperi* and *Philhedra*. All these were present as 1% or less of the assemblage, except for *Petrocrania* which alone constituted 13.8% of the assemblage. Wright (1970) also recorded *Eoplectodonta*, but this genus is essentially indistinguishable from *Sowerbyella* except for the presence of denticles along the hinge line. No specimens in this study showed evidence of such denticles.

The older fauna from Grange Hill House Cottage (Table 10) is somewhat anomalous in comparison with the other

Table 8 Total assemblage collected from Kildare, Grange Hill Horizon 1.

| | Internal | | | | External | | | | Total | |
	PV	BV	C	I	PV	BV	C	I	no.	%
BRACHIOPODS										
Acanthocrania?	1	–	–	–	–	1	–	–	1	0.15
Chonetoidea sp.	1	–	1	–	–	–	1	–	3	0.5
Cremnorthis parva	57	76	4	–	10	21	5	–	85	13.2
dalmanellids, indet.	23	3	3	–	7	2	–	2	27	4.2
Hedstroemina sp.	3	–	–	–	3	3	–	–	3	0.5
Kjerulfina?	1	–	–	–	–	–	–	–	1	0.15
Kullervo aff. *hibernica*	2	–	–	–	1	–	–	–	2	0.3
Leptaena sp.	6	–	1	–	3	5	–	6	10	1.5
Leptestiina oepiki	7	2	–	–	–	–	–	–	7	1.0
Lingulella ovata	–	–	–	–	–	–	–	3	3	0.5
Nicolella cf. *actoniae*	–	1	–	–	–	1	–	–	1	0.15
'Orthambonites' sp.	2	6	–	–	2	–	–	–	6	0.9
Orthisocrania divaricata	38	23	–	68	–	–	–	108	92	14.2
Petrocrania harperi	–	89	–	–	–	30	–	–	89	13.8
Philhedra sp.	–	–	–	–	–	1	–	–	1	0.15
Platystrophia sp.	31	34	6	–	18	13	10	13	57	8.8
Rhactorthis sp.	1	3	1	–	1	2	1	–	5	0.8
Skenidioides costatus	109	32	1	–	20	15	3	–	113	17.5
Sowerbyella sericea	28	17	1	–	12	19	1	6	33	5.1
Strophomena?	2	–	–	–	1	–	–	–	2	0.3
TRILOBITES										
Autoloxolichas cephala									3	0.5
Calyptaulax pygidium									1	0.15
Flexicalymene cephalon									1	0.15
OTHER ELEMENTS										
crinoid ossicles (7)									1	0.15
gastropods									50	7.7
ramose bryozoans									4	0.6
prasoporid bryozoans									8	1.2
tentaculitids									29	4.5
orthocones									4	0.6
bivalves									2	0.3
conulariids									1	0.15
sponge spicule									1	0.15
Total									646	99.85

Table 9 Total assemblage collected from Kildare, Grange Hill Horizon 2.

| | Internal | | | | External | | | | Total | |
	PV	BV	C	I	PV	BV	C	I	no.	%
BRACHIOPODS										
dalmanellids, indet.	2	3	–	–	–	1	–	–	3	5.1
Hedstroemina sp.	7	–	–	–	1	–	–	–	7	11.9
Leptaena?	1	1	–	–	1	2	–	–	2	3.3
Lingulella ovata	–	–	1	–	–	–	–	16	9	15.3
Orthisocrania divaricata	1	3	–	1	–	–	–	2	5	8.5
Petrocrania harperi	–	2	–	–	–	4	–	–	4	6.8
Platystrophia sp.	–	1	–	–	–	2	–	1	3	5.1
Salopia?	–	1	–	–	–	–	–	–	1	1.7
Skenidioides costatus	3	–	–	–	–	–	–	–	3	5.1
Sowerbyella sericea	2	–	–	–	–	–	–	–	2	3.3
OTHER ELEMENTS										
orthocone									3	5.1
prasoporid bryozoan									3	5.1
bivalve									1	1.7
gastropods									13	22.0
Total									59	100.0

PV = pedicle valves, BV = brachial valves, C = conjoined valves, I = indeterminate valves, NO. = equivalent number of total animals. (N.B. Numbers in brackets are total fragments of colonial or fragmented individuals – see discussion). See discussion on p.127.

PV = pedicle valves, BV = brachial valves, C = conjoined valves, I = indeterminate valves, NO. = equivalent number of total animals. (N.B. Numbers in brackets are total fragments of colonial or fragmented individuals – see discussion). See discussion on p.127.

Table 10 Total assemblage collected from Kildare, Grange Hill House Cottage.

	Internal PV BV C I	External PV BV C I	Total no.	%
BRACHIOPODS				
dalmanellids, indet.	– – – –	2 1 – –	2	0·4
Dolerorthis?	1 – – –	– – – –	1	0·2
Hibernodonta?	– 3 – –	2 1 – 3	4	0·8
Leangella?	1 – – –	– – – –	1	0·2
Leptaena sp.	1 – – –	– – – –	1	0·2
lingulid, indet.	– – – –	– – – 4	4	0·8
Oanduporella cf. *reticulata*	13 10 – –	9 6 – –	13	2·5
Petrocrania?	– 2 – –	– 1 – –	2	0·4
Plaesiomys multiplicata	26 13 – –	12 20 – –	26	5·0
Rafinesquina sp.	8 9 – 2	10 5 – 4	12	2·3
Skenidioides sp.	3 1 – –	– 2 – –	3	0·6
TRILOBITES				
Flexicalymene sp. pygidia			2	0·4
Flexicalymene sp. cephala			4	0·8
Autoloxolichas cephala			3	0·6
Ampyx sp. pygidium			1	0·2
OTHER ELEMENTS				
bivalve species (106)			53	10·1
gastropod species			246	47·2
ostracods (*Tetradella?*) (132)			66	12·7
crinoid ossicles (19)			1	0·2
orthocone fragments (15)			15	2·9
tentaculitids			1	0·2
bryozoans			45	8·6
'*Mastopora*'?			15	2·9
Total			521	100·2

PV = pedicle valves, BV = brachial valves, C = conjoined valves, I = indeterminate valves, NO. = equivalent number of total animals. (N.B. Numbers in brackets are total fragments of colonial or fragmented individuals – see discussion). See discussion on p.127.

Leinster faunas. It is molluscan not brachiopod dominated, with different brachiopod genera present. Five of the 11 genera are not known from the other localities and make up 10·8% of the fauna, of which only 13·4% comprises brachiopods. The fossils were excavated from muddy and tuffaceous siltstones and fine sandstones at the back of the cottage. About 2–3 metres below the fossiliferous section are fine quartz pebble conglomerates with fragments of the underlying slates.

The fossils are interpreted as having lived in a shallow water but low energy environment, perhaps close to the shore of the emergent volcanic cone of Grange Hill. Supporting evidence includes the very close proximity of lavas interpreted as being subaerial, and the abundance of an ostracod (*Tetradella?*) which elsewhere is commonly indicative of intertidal or shallow subtidal conditions.

Kilbride, within the Upper Tramore Volcanic Formation, by contrast, represents a different setting. In the small exposure there are contorted streaks and lenses of tuff in the dark siltstones, with very obscure bedding. The faunal evidence from this work and the limited field evidence supports Carlisle's (1979: 551) interpretation of slumped volcaniclastics, and that the lithology is a debris flow. The high diversity and low frequency of any one species suggests that faunas from different areas and substrates were 'sampled' in the downslope movement of the sediment mass. Although Carlisle (1979: 552) only listed certain genera as common and

others as 'also in the fauna', the assemblage listed in Table 11 shows significant differences, reflecting a different sample. In the fauna are numerous (22) fragmentary plates of a cheirocrinid cystoid, of which 5 may be oral plates. These may belong (C.R.C. Paul, personal communication 1987) to *Hadrocystis* or *Acantholepis* (whose sole species *A. jamesi* M'Coy, 1846 was described from Raheen, Waterford Harbour). The preservation of the cheirocrinids (Plate 16, figs 12-18), which are fractured across plates and not along boundaries, also reflects the disturbed nature of this horizon. There are also 9 plates of *Echinosphaerites*, some of which are broken. Comparable examples of debris flows include that described by Lockley (1984) from Builth, central Wales and Kilbucho in Scotland (Clarkson *et al.*1992).

Although it is reasonable to treat them as '*in situ*' faunas

Table 11 Total assemblage collected from Kilbride.

	Internal PV BV C I	External PV BV C I	Total no.	%
BRACHIOPODS				
Acanthocrania?	– – – –	– 1 – –	1	0·6
Anisopleurella?	– 1 – –	– 1 – –	1	0·6
Bicuspina?	– 2 – –	– 1 – –	2	1·1
Bimuria sp.	27 – – –	1 – – –	27	15·0
Chonetoidea cf. *abdita*	14 6 – –	9 2 – –	14	7·8
Cremnorthis parva	8 7 – –	1 3 – –	8	4·5
dalmanellids, indet.	1 – – –	2 2 1 –	3	1·7
Hesperorthis sp.	3 – – –	– – – –	3	1·7
Leptestiina oepiki	6 6 – –	1 2 – –	6	3·3
lingulid, indet.	– – – –	– – – 1	1	0·6
Nicolella cf. *actoniae*	10 – – –	8 6 – –	10	5·6
'*Orthambonites*' sp.	8 14 – –	1 3 – –	14	7·7
Platystrophia sp. 2	1 3 – –	1 1 – –	3	1·7
Porambonites sp.	2 – – –	– – – –	2	1·1
Salopia?	1 – – –	– – – –	1	0·6
Saukrodictya sp.	1 – – –	1 – – –	1	0·6
Schizotreta sp.	1 – – –	1 – – –	1	0·6
Skenidioides costatus	4 4 – –	4 7 – –	7	3·9
Sowerbyella sericea	18 7 – –	13 10 – –	18	10·0
sowerbyellid, indet.	2 – – –	– – – –	2	1·1
TRILOBITES				
cybelinid cephalon			1	0·6
lichid cephalon			1	0·6
Arthrorhachis?			1	0·6
cybelinid librigenae (5)				
illaenid? cephalon			1	0·6
Xylabion? pygidium			1	0·6
OTHER ELEMENTS				
sponge?			1	0·6
gastropods			6	3·3
ostracods			3	1·7
orthocone			1	0·6
conulariids			2	1·1
prasoporid bryozoans			16	8·9
ramose bryozoans (27)			1	0·6
coral?			1	0·6
crinoid ossicles (77)			1	0·6
cheirocrinid cystoid			17	9·4
cheirocrinid cystoid oral plates? (5)				
Echinosphaerites plates (8)			1	0·6
Total			179	100·8

PV = pedicle valves, BV = brachial valves, C = conjoined valves, I = indeterminate valves, NO. = equivalent number of total animals. (N.B. Numbers in brackets are total fragments of colonial or fragmented individuals – see discussion). See discussion on p.127.

for stratigraphical correlation, the loose block nature of assemblages from Ballykale (Table 12) and Clologe (Table 13) offers little information, although the fauna from Clologe is from two distinct lithologies, one shaly and one tuffaceous. Hiller's (1971) collections from Frankfort and Clogh also came from loose blocks. Carrigadaggan, although yielding a diverse large assemblage (Table 14), gave little information about palaeoecology, since exposure was poor and much material came from broken blocks not completely *in situ*. The coarse volcaniclastic lithology preserved details of the fossils only poorly.

The presence of *Echinosphaerites* cf. *granulatus* M'Coy (Plate 16. figs 1–7,9–10) in some abundance at Carrigadaggan, is worthy of note. It was listed as *E. aurantium* in the G.S.I. Memoir (Kinahan 1879). This species is found as almost complete individuals (6 specimens), suggesting rapid burial as in a coarse tuff fall, but there are also numerous isolated (15) or several associated plates (27) of the cystoid. Forbes (1848) monographed the British and Irish cystoid fauna, and Paul (1973, 1984) has produced a modern revision of some diploporite and rhombiferan cystoids. This material, which has been confirmed as *Echinosphaerites* (personal communication 1987) will be dealt with in the third part of Paul's monograph. Bockelie (1981) has recently reviewed the functional morphology and evolution of the genus, from many different lithologies in Russia and Scandinavia. In spite of the fact that there are several nearly complete thecae, the fact that few if any preserve evidence of a stem, cover plates of the gonopore, brachioles or oral cover plates, suggests that they were not covered by sediment immediately after death. It is difficult to be unequivocal about these taphonomic factors, or the loss of periproctal plates (which occurred in less than 5% of specimens reviewed by Bockelie, 1981: 191), since the Carrigadaggan lithology is so coarse-grained that fine detail of the plates is not always preserved. Two specimens show projections, however, one of which is believed to be an oral projection, the other possibly the basal plates to which the stolon was attached (see Plate 16, figs 7, 9, 10). Possibly the most likely explanation is that *Echinosphaerites* and the cheirocrinid cystoids, of which there are 9 fragmentary plates similar to the Kilbride material (Plate 16, figs 8,11), were buried rapidly by volcaniclastic material but were subject to current action in shallow waters rather than inundated by distal tuff falls.

Ballygarvan Bridge (Table 15) has volcanic rocks adjacent, but exposure is too poor and the sample is too limited to infer much. As previously noted, volcanic events may best account for the differences between the new collections from Raheen and the G.S.I. records (Baily *in* Kinahan 1882: 38–39). A diverse fauna of 25 species including 9 trilobites in abundance was recorded, whilst new collections (Table 16) are over-whelmingly dominated by a dalmanellid (probably *Howellites*, but remaining indeterminate because of the strong deformation) with only a few trilobites and generally low diversity. Tuff horizons (tens of cm thick) are common in the new section that was exposed and almost certainly account for apparent differences.

The Greenville assemblage (Table 17) also differs from earlier collections. Since this was collected by digging beneath a thick farmyard deposit it is most likely that different horizons were sampled, but the cause of the changes in assemblages from horizons in close succession remains unknown. In contrast, the collections from Greenville-Moyne (Table 18) probably came from the same horizon as that

Table 12   Total assemblage collected from Ballykale.

	Internal				External				Total	
	PV	BV	C	I	PV	BV	C	I	no.	%
Bimuria cf. *dyfiensis*	59	10	–	–	16	5	–	–	59	81·0
Chonetoidea	1	–	–	–	–		–	–	1	1·3
dalmanellids, indet.	2	–	1	–	1	1	1	–	3	4·2
Leptestiina sp.	2	–	–	–	–	–	–	–	2	2·7
Platystrophia	–	1	–	–	–	–	–	1	2	2·7
Ptychoglyptus	1	–	–	1	1	–	–	–	2	2·7
Saukrodictya sp.	1	–	–	–	–	–	–	–	1	1·3
Sowerbyella?	–	–	–	–	2	–	–	–	2	2·7
strophomenid, indet.	–	–	–	–	–	–	–	1	1	1·3
Total									73	99·9

OTHER ELEMENTS
ramose bryozoans (5)
trilobite genal spines? (3)
trilobite thoracic segments (2)

PV = pedicle valves, BV = brachial valves, C = conjoined valves, I = indeterminate valves, NO. = equivalent number of total animals. (N.B. Numbers in brackets are total fragments of colonial or fragmented individuals – see discussion). See discussion on p.127.

Table 13   Total assemblage collected from Clologe Upper.

	Internal				External				Total	
	PV	BV	C	I	PV	BV	C	I	no.	%
BRACHIOPODS										
Anisopleurella?	1	–	–	–	1	–	–	–	1	1·4
dalmanellids, indet.	2	4	1	–	6	5	–	–	7	10·0
Dolerorthis?	1	1	–	–	1	–	–	–	1	1·4
Glyptorthis	–	–	–	–	–	–	–	1	1	1·4
Kjaerina?	–	–	–	1	–	–	–	1	1	1·4
Leptestiina sp.	1	2	1	–	–	–	–	–	3	4·3
Nicolella sp.	2	1	–	–	2	1	–	–	2	2·9
Oanduporella?	–	–	–	–	–	2	–	–	2	2·9
Plaesiomys?	–	–	–	–	–	–	–	1	1	1·4
Ptychoglyptus sp.	–	–	–	1	–	–	–	1	1	1·4
Salopia?	–	–	–	–	–	1	–	–	1	1·4
Skenidioides sp.	1	–	–	–	1	–	–	–	1	1·4
Sowerbyella sp.	2	–	–	–	–	–	–	–	2	2·9
strophomenid, indet.	–	–	–	1	–	–	–	2	1	1·4
TRILOBITES										
tretaspid cephala									18	25·7
tretaspid cephalon fragments (14)										
cybelinid librigenae (2)										
agnostid									1	1·4
lichid cephalon									1	1·4
cheirurid cephalon									1	1·4
OTHER ELEMENTS										
ramose bryozoans (4)									1	1·4
prasoporid bryozoans									1	1·4
orthocone									1	1·4
crinoid ossicles (4)									1	1·4
gastropods									12	17·2
conulariid									1	1·4
coral?									1	1·4
cheirocrinid cystoids									3	4·3
Echinosphaerites plates (4)										
Echinosphaerites theca									1	1·4
cystoid, indet.									2	2·9
Total									70	96·8

PV = pedicle valves, BV = brachial valves, C = conjoined valves, I = indeterminate valves, NO. = equivalent number of total animals. (N.B. Numbers in brackets are total fragments of colonial or fragmented individuals – see discussion). See discussion on p.127.

Table 14 Total assemblage collected from Carrigadaggan.

| | Internal | | | | External | | | | Total | |
	PV	BV	C	I	PV	BV	C	I	no.	%
BRACHIOPODS										
Bicuspina?	–	–	1	–	–	–	–	–	1	0·3
Bimuria?	–	–	–	–	–	1	–	–	1	0·3
Cremnorthis parva	5	3	1	–	1	1	–	–	6	1·6
dalmanellids, indet.	47	14	4	–	25	17	–	–	51	13·2
Dolerorthis?	1	2	–	–	–	–	–	–	2	0·5
Glyptorthis?	–	–	–	–	–	–	–	1	1	0·3
Kullervo aff. *hibernica*	3	2	–	–	3	1	–	4	5	1·3
Leptellina cf. *llandeiloensis*	4	3	–	–	–	–	–	–	4	1·0
Leptestiina oepiki ampla	29	10	–	–	4	4	–	–	29	7·5
lingulid, indet.	–	–	–	–	–	–	–	4	2	0·5
Nicolella cf. *actoniae*	–	–	–	–	–	7	–	–	7	1·8
'Orthambonites' sp.	4	11	–	–	2	4	–	–	11	2·8
Orthisocrania divaricata	1	1	–	–	–	–	–	5	4	1·0
Oxoplecia?	–	1	–	–	–	1	–	1	2	0·5
Platystrophia sp.	5	7	1	–	3	1	1	–	9	2·3
plectambonitacean, indet.	–	–	–	–	–	2	–	–	2	0·5
Salopia?	1	1	–	–	–	–	–	–	1	0·3
Saukrodictya cf. sp. A	1	–	–	–	3	1	–	4	5	1·3
Skenidioides costatus	3	–	–	–	–	2	–	–	3	0·8
Sowerbyella sericea	–	2	–	–	1	4	–	–	4	1·0
triplesiid indet. 1	–	–	1	–	–	–	–	–	1	0·3
triplesiid indet. 2	2	–	–	–	–	–	–	–	2	0·5
TRILOBITES										
trinucleid pygidia (1)										
trinucleid cephala									5	1·3
Atractopyge pygidia									18	4·6
Atractopyge cephala (9)										
cybelinid librigenae (15)										
lichid cephala									2	0·5
illaenid? cephala									1	0·3
Calyptaulax? cephalon									1	0·3
OTHER ELEMENTS										
prasoporid bryozoans									75	19·4
ramose bryozoans									42	10·8
gastropod species									29	7·5
conulariids									27	7·0
bivalves									2	0·5
crinoid ossicles (46)									1	0·3
orthocones									11	2·8
coral?									1	0·3
Echinosphaerites single plates (15)										
Echinosphaerites attached plates (27)									5	1·3
Echinosphaerites thecae									5	1·3
cheirocrinid cystoid									9	2·3
Total									387	100·1

PV = pedicle valves, BV = brachial valves, C = conjoined valves, I = indeterminate valves, NO. = equivalent number of total animals. (N.B. Numbers in brackets are total fragments of colonial or fragmented individuals – see discussion). See discussion on p.127.

Table 15 Total assemblage collected from Ballygarvan Bridge.

| | Internal | | | | External | | | | Total | |
	PV	BV	C	I	PV	BV	C	I	no.	%
BRACHIOPODS										
dalmanellid, indet.	4	1	–	–	5	1	–	–	5	6·75
Lingulella ovata	–	–	–	–	–	–	–	3	2	2·7
Nicolella cf. *actoniae*	1	–	–	–	1	–	–	–	1	1·35
Platystrophia sp.	1	1	–	–	1	1	–	–	1	1·35
Salopia?	1	1	–	–	1	1	–	–	1	1·35
Skenidioides sp.	1	–	–	–	1	–	–	–	1	1·35
Sowerbyella sp.	–	1	–	–	–	1	–	–	1	1·35
TRILOBITES										
calymenid pygidium									1	1·35
Deacybele cephalon									1	1·35
OTHER ELEMENTS										
prasoporid bryozoans									20	27·0
ramose bryozoans (2)									1	1·35
gastropods									37	50·0
tentaculitid									1	1·35
Echinosphaerites theca									1	1·35
Total									74	99·95

PV = pedicle valves, BV = brachial valves, C = conjoined valves, I = indeterminate valves, NO. = equivalent number of total animals. (N.B. Numbers in brackets are total fragments of colonial or fragmented individuals – see discussion). See discussion on p.127.

Table 16 Total assemblage collected from Raheen.

| | Internal | | | | External | | | | Total | |
	PV	BV	C	I	PV	BV	C	I	no.	%
BRACHIOPODS										
Chonetoidea sp.	3	1	–	–	2	–	–	1	4	2·9
dalmanellid (*Howellites*?)	76	44	–	–	61	54	5	–	81	59·6
Porambonites?	1	–	–	–	–	–	–	–	1	0·7
strophomenid, indet.	2	–	1	–	2	–	–	–	3	2·2
TRILOBITES										
Ampyx pygidia									2	1·5
Tretaspis cephalon									1	0·7
tretaspid cephalon									1	0·7
tretaspid cephalic fragments (2)										
tretaspid pygidium (1)										
OTHER ELEMENTS										
crinoids (5)									1	0·7
gastropods									36	26·5
ostracods									2	1·5
conulariids									2	1·5
orthocones									2	1·5
Total									136	100·0

PV = pedicle valves, BV = brachial valves, C = conjoined valves, I = indeterminate valves, NO. = equivalent number of total animals. (N.B. Numbers in brackets are total fragments of colonial or fragmented individuals – see discussion). See discussion on p.127.

recorded by Brenchley *et al.* (1977) and slightly increase the genera known from here.

Ballinatray (Table 19) preserves a rare occurrence of shelly fossils in a normally graptolitic facies. Coastal sections of the Ballinatray Formation north of Courtown have hitherto yielded only graptolites (Crimes & Crossley 1968, Brenchley & Treagus 1970). Shells are found in thin, densely packed bands in calcareous slates. Restricted exposure in the bed and banks of the Owenavorragh River and strong deformation make assessment difficult, but the lack of size variation, restricted diversity and dense packing suggest that the fauna

was a coquina. Whether long distance transport or local winnowing was involved is not clear, but all specimens are small including the rare genera, elsewhere of a normally larger size.

Table 17 Total assemblage collected from Greenville.

| | Internal | | | | External | | | | Total | |
	PV	BV	C	I	PV	BV	C	I	no.	%
BRACHIOPODS										
Chonetoidea abdita	24	25	–	1	31	47	–	27	61	41·5
dalmanellids, indet.	–	–	–	–	4	1	–	–	4	2·7
Oanduporella?	1	–	–	–	3	1	–	–	3	2·0
TRILOBITES										
Remopleurides sp. cephala									5	3·4
Homalopteon sp. pygidium									1	0·7
Ampyx austinii cephala (8)										
Ampyx austinii glabellar spines (7)										
Ampyx austinii pygidia									16	10·9
'*Trinodus*' *agnostiformis* pygidia?									8	5·4
Tretaspis cephalon									1	0·7
trinucleid cephala									4	2·7
trinucleid pygidia (2)										
trinucleid thoraces (2)										
trinucleid genal spines (2)										
OTHER ELEMENTS										
cheirocrinid cystoid									1	0·7
gastropods									38	25·9
bivalve									1	0·7
conulariids									4	2·7
Total									147	100·0

PV = pedicle valves, BV = brachial valves, C = conjoined valves, I =
indeterminate valves, NO. = equivalent number of total animals. (N.B.
Numbers in brackets are total fragments of colonial or fragmented individuals
– see discussion). See discussion on p.127.

Comparisons and contrasts with coeval associations

A prerequisite to recognition of faunal provinciality in brachiopod assemblages is the determination of whether apparently different faunas are simply facies controlled. This was undertaken as an integral part of this project and is briefly summarised here. Due to the problems noted before, only some localities yielded assemblages which could be treated as palaeocommunities. These were Grange Hill Horizon 1, Grange Hill House Cottage, Carrigadaggan, Raheen, Greenville and Greenville-Moyne.

In fact, the assemblages are clearly dissimilar to platform sequence faunas from Laurentia, and to the marginal Scoto-Appalachian faunas from Ireland and Britain. Few assemblages of similar age from the Lake District are known and there are no modern quantitative studies for direct comparison. Essentially, only comparisons with Anglo-Welsh associations were applicable. Principal Component Analysis (PCA) using Palstat (Harper & Ryan 1987) is an effective way of discriminating and illustrating the elements which contribute most to the variation between samples. One example is given to illustrate the comparitive analysis undertaken. Figure 15 shows a plot of vector 1 against vector 3 for the Grange Hill Horizon 1 association and 11 samples of the *Nicolella* Association from the Gelli-grin Formation from Lockley (1980). Plots of vector 1 against 2 discriminated abundance trends of dalmanellids. The plot in Fig. 15 clearly differentiated the Grange Hill elements as contributing substantially to the variation on vector 3. Whilst not a precise test, it shows important differences which do not permit the association to be considered as an equivalent to the *Nicolella* Association,

Table 18 Total assemblage collected from Greenville-Moyne.

| | Internal | | | | External | | | | Total | |
	PV	BV	C	I	PV	BV	C	I	no.	%
BRACHIOPODS										
Anisopleurella sp.	8	2	–	–	2	5	–	–	8	6·0
Cremnorthis parva	8	2	–	–	–	–	–	–	8	6·0
dalmanellids, indet.	39	16	6	–	19	17	–	–	45	33·6
Dolerorthis?	1	1	–	–	–	–	–	–	1	0·75
Kullervo aff. *hibernica*	3	–	–	–	3	2	–	2	4	3·0
Leptestiina oepiki	3	2	–	–	–	–	–	–	3	2·2
lingulid, indet.	–	–	–	–	–	–	–	–	11	0·75
Nicolella cf. *actoniae*	3	4	1	–	4	7	–	–	8	6·0
'*Orthambonites*'?	5	4	–	–	1	1	–	–	5	3·7
Orthisocrania?	–	–	–	–	–	–	–	1	1	0·75
plectambonitacean, indet.	–	–	–	–	–	–	–	2	1	0·75
Rhactorthis?	1	–	–	–	1	–	–	–	1	0·75
Salopia sp.	–	4	–	–	–	1	–	–	4	3·0
Saukrodictya cf. sp. A	–	–	–	–	–	–	–	2	1	0·75
Skenidioides costatus	1	–	–	–	1	–	–	–	1	0·75
Sowerbyella?	3	–	–	–	2	1	–	–	3	2·2
strophomenid, indet.	–	1	–	–	–	1	–	–	1	0·75
TRILOBITES										
cybelinid? librigenae (8)										
indet. pygidia (1)										
indet. cephala (2)									2	1·5
OTHER ELEMENTS										
crinoid ossicles (14)									1	0·75
prasoporid bryozoans									22	16·4
ramose bryozoans									7	5·25
cheirocrinid cystoids									3	2·2
ostracods									3	2·2
Total									134	100·0

PV = pedicle valves, BV = brachial valves, C = conjoined valves, I =
indeterminate valves, NO. = equivalent number of total animals. (N.B.
Numbers in brackets are total fragments of colonial or fragmented individuals
– see discussion). See discussion on p.127.

Table 19 Total assemblage collected from Ballinatray.

| | Internal | | | | External | | | | Total | |
	PV	BV	C	I	PV	BV	C	I	no.	%
BRACHIOPODS										
Chonetoidea sp.	1	–	–	–	–	–	–	–	1	1·8
dalmanellids, indet.	38	26	–	–	8	10	–	14	45	78·9
Dolerorthis?	1	2	–	–	–	–	–	–	2	3·5
Leptestiina sp.	1	1	–	–	–	–	–	–	1	1·8
plectambonitacean, indet.	1	2	–	–	–	–	–	3	4	7·0
Sowerbyella?	1	–	–	–	–	–	–	–	1	1·8
TRILOBITES										
Encrinuroides? pygidia									2	3·5
OTHERS										
crinoid ossicle									1	1·8
Total									57	100·1

PV = pedicle valves, BV = brachial valves, C = conjoined valves, I =
indeterminate valves, NO. = equivalent number of total animals. (N.B.
Numbers in brackets are total fragments of colonial or fragmented individuals
– see discussion). See discussion on p.127.

sensu Lockley (1980). Principal of these are the abundance of the calcareous inarticulates *O. divaricata* and *P. harperi*, and the much greater frequency of *Skenidioides* and *Cremnorthis* at Kildare than in the Welsh Longvillian.

Pickerill & Brenchley (1979) studied the faunal communities of the south Berwyn Hills of N. Wales, and defined communities very similar to those of Lockley (1980). Direct comparison using PCA was not possible due to their data presentation. For their *Nicolella* Community simple inspection shows that the Grange Hill association does not equate (Table 20). This aspect of the study highlighted the benefits of recording raw palaeontological data, as suggested by Lockley (1980: 167). As Jaannusson (1984: 127) noted, there are many published studies which cannot be compared because of differences in tabulation of quantitative data. The example of the Grange Hill Horizon 1 assemblage compared with the Welsh *Nicolella* Association is a typical one. The analysis of the suitable assemblages from Leinster in relation to Welsh and English Caradoc (Hurst 1979a, 1979b, Pickerill & Brenchley 1979, Lockley 1980) and especially Lockley's (1983) rigorous definition of eight palaeocommunities is discussed in more detail in Parkes (1990). The moderate to severe differences evident precluded placement of the Leinster assemblages into those palaeocommunities.

The localities from Leinster are in volcano-sedimentary sequences associated with island arc volcanism. The rapid facies changes over short distances, with little or no shelf development and invasion of volcanic detritus into clastic substrates are sufficient to explain this lack of comparable

Table 20 Nucleus of *Nicolella* Community as defined by Pickerill & Brenchley (1979), compared to nucleus of Grange Hill Horizon 1 association.

Nicolella Community		Kildare, Grange Hill, Horizon 1	
Nicolella	34%	*Skenidioides*	18%
Dolerorthis	21%	*Orthisocrania*	14%
Platystrophia	16%	*Petrocrania*	14%
Skenidioides	9%	*Cremnorthis*	13%
Leptestiina	6%	*Platystrophia*	9%
Eoplectodonta	4%	gastropods	8%
Howellites	3%	*Sowerbyella*	5%
Sowerbyella	3%	tentaculitids	4%
Cremnorthis	<1%	dalmanellids, indet.	4%

community development. Lockley (1983) concluded that the Welsh Basin, with low facies gradients for much of the Ordovician rather than basin margin localities, provided more stable sites for the evolution of diverse, well established palaeocommunities.

Biogeography

The component brachiopod species of the Duncannon Group assemblages are best understood when viewed in terms of species migrations and palaeogeographical changes. Harper and Parkes (1989), Harper *et al.* (1991) and Murphy *et al.* (1991) have dealt partially with the faunas described here. A more complete treatment of their biogeographical context is contained in Parkes (1992) and is not reiterated here.

In summary, these faunas are ascribed to a distinct Anglo Welsh Province centred on Eastern Avalonia in the Caradoc. Despite the lack of comparable palaeocommunity development, there are numerous congeneric and conspecific forms, many with an earlier origin in migrations from the Baltic Province. Specific appearances of Scoto-Appalachian e.g. *Leptellina* and *Bimuria*, and Mediterranean Province genera e.g., *Saukrodictya*, can also be tracked as provinciality was diminished by northward movement of Avalonia towards Laurentia and low latitudes (Fig. 16, p.146). They are also significant in constraining volcanic and tectonic events. Lavas at Grange Hill, Kildare are tightly constrained to the Soudleyan – Longvillian interval. Although the stratigraphical position of the other faunas is not so clear, the data from this study support recent ideas that subduction-related volcanism ceased in the mid Caradoc (Pickering *et al.* 1988, Leat & Thorpe 1989). The biogeographical analysis of Ordovician faunas is an important facet of understanding the development of the Caledonides by Iapetus closure. Discovery of new assemblages may provide new evidence, but revision of faunas from old localities such as this work and Parkes (1992) is equally important. Furthermore, new methods of analysis such as seriation (Parkes *et al.* 1990) may also reveal clearer distribution patterns.
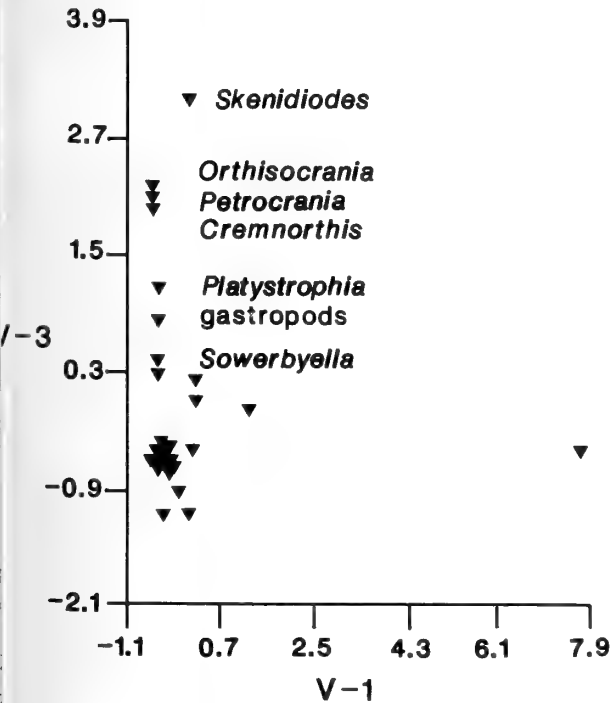
Fig. 15 Principal Component Analysis of Kildare Grange Hill Horizon 1 association with Gelli-grîn Formation *Nicolella* Association samples: plot of vector 1 against vector 3. *Data sources*: Association 1: Table 8 (p. 128), Grange Hill Horizon 1. Associations 2–11, Gelli-Grîn Formation. From Lockley, 1980: fig. 12 (GG1h, GG1g1, GG1b); fig. 13 (GG2d, GG2b); fig. 14 (TB 16, TB 12); fig. 15 (R34, R30, R28).

SYSTEMATIC PALAEONTOLOGY

For the better preserved, larger samples, the 'material' section of each description includes only the measured sample on which the statistical data are based and excludes
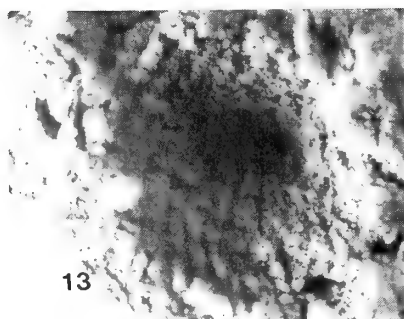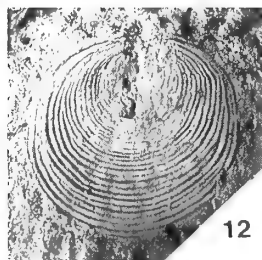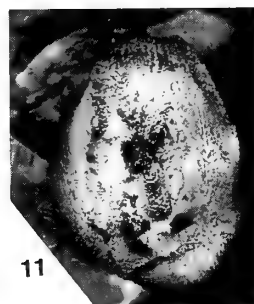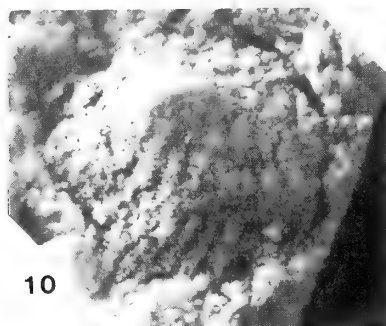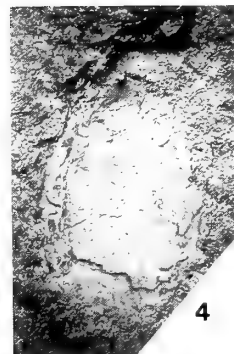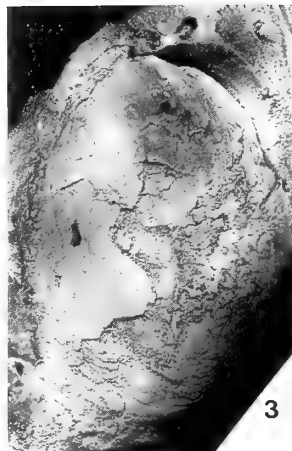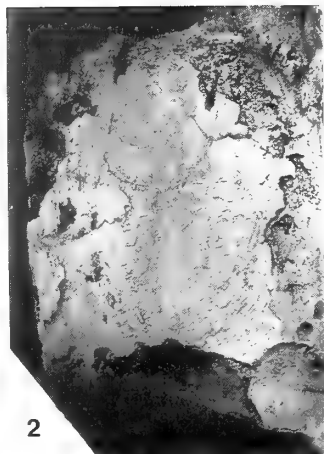
the fragmentary material included in the Tables 8–19. For some genera the available material did not merit a full taxonomic statistical description. In these cases the best representative forms are figured, and for this material dimensions are given in the systematic section, if the magnification is not an adequate indication. Full data sets are given for any statistically described species in a supplementary document lodged at The Natural History Museum (see p.118) or available from the author. In addition to the material described or noted in this section, there were some poorly preserved or fragmentary specimens, often of questionable identity, which were not worthy of discussion but are listed in the locality Tables (8–19). Inevitably, for each locality there were a few unidentified specimens.

In this study, the dalmanelloid brachiopods were a common, albeit minor, element of most faunas. Although species lineages are stratigraphically useful (e.g. Hurst 1979a), the recognition of different genera and species is dependent on the measurement of small morphological variations in the cardinalia, musculature and shell outline, as well as aspects of the costellate ornamentation. In the localities sampled by me, dalmanelloids were present in most cases, although as minor constituents of the assemblage, except at Raheen where one species was dominant. Their poor preservation, small sample numbers and frequent tectonic deformation made it difficult to make confident identifications; they are therefore listed as 'indeterminate dalmanellids' in the relevant tables. The identification of the less common elements in the faunas, such as bivalves, ostracods, gastropods and crinoids was outside the scope of the project, and in any case most material was poorly preserved and generic identification would have been somewhat equivocal. However, a few elements such as the cystoid *Echinosphaerites* are figured.

All material, other than that figured, is housed in the James Mitchell Museum (JMM) in the Department of Geology, University College Galway. The systematic classification of the Brachiopoda is based largely on Cocks (1978), and Cocks & Rong (1989) for the Plectambonitoidea.

Phylum **BRACHIOPODA**
Class **INARTICULATA** Huxley, 1869
Order **LINGULIDA** Waagen, 1885
Superfamily **OBOLOIDEA** King, 1846
Family **OBOLIDAE** King, 1846
Subfamily **LINGULELLINAE** Schuchert, 1893
Genus *LINGULELLA* Salter, 1866

Lingulella ovata M'Coy, 1846   Pl. 1, figs 1–9, 11, 14

1846   *Lingula ovata* M'Coy: 24; pl. 3, fig. 1.
1866   *Lingula ovata* M'Coy; Davidson: 38; pl. 2, figs 19–23.
1866   *Lingula obtusa* Hall?; Davidson: 52; pl. 3, figs 31, 32.

cf. 1963   *Lingulella* cf. *ovata* (M'Coy); Williams: 344; pl. 1, figs 1–3.
    1978   *Lingulella ovata* M'Coy; Cocks: 15, 171, 172.
cf. 1980   *Lingulella* cf. *ovata* (M'Coy); Lockley: 203, fig. 25.
cf. 1980   *Lingulella* sp. A; Hiller: 123, figs 11–15.

MATERIAL AND LOCALITY. Kildare, Grange Hill, Horizon 2: 8 single valves, 1 conjoined pair of valves.

DESCRIPTION. *Exterior.* Very large equally biconvex, elongately oval valves with acute beak. Maximum width at 66% of length although sides nearly parallel. Shell variably buff, brown and black coloured, ornamented with fine concentric growth lines on lateral and anterior margins, nearly smooth centrally. Occasional faint radial striations medially towards anterior margin. Depth of valves 10% of length. Width is 60% of length.

Ventral interior. Not positively known, but one specimen shows smooth surface with faint median striations towards anterior margin.

Dorsal interior. Two specimens show dorsal median septum, extending 50% and 70% of the length, expanding in width and height anteriorly. The growth lines are deflected anteriorly by the median septum.

DISCUSSION. M'Coy (1846) described the species from three localities; Ballygarvan Bridge, Kildare and Newtown Head, Co. Waterford. Cocks (1978) selected the lectotype (NMING:F4578) from the Chair of Kildare. He stated it was from the Kildare Limestone Formation (Rawtheyan), but M'Coy recorded it as 'common in the shale of Chair of Kildare' which is actually the lithology of the Grange Hill locality. The opportunity is taken here to figure some good topotype material. The Griffith Collection specimen in the N.M.I. (F5482), a paralectotype from Ballygarvan Bridge, accords with the type material in its proportions, although it is only the anterior half of a valve. A significant feature revealed by a larger sample is the very large size which this species can attain. M'Coy (1846) records the length as one inch three lines (c. 32 mm) but the largest specimen collected is 43 mm long, although much smaller specimens are also present. It appears that this large size is probably normal for the species rather than representing a population which realised optimal conditions for growth, as suggested by Pickerill (1973) in a study of *Lingulasma tenuigranulata* from North Wales. Harper (1984: 19), in noting the similarity of *L. carrickensis carrickensis* to *L. ovata*, raised the problems of Ordovician *Lingulella* taxonomy. The sample described here may help facilitate a future multivariate morphometric analysis of described species. Moreover *L. ovata* may prove ultimately to be a synonym of *L. brevis* (Portlock, 1843), as noted by Mitchell (1977). The relative proportions are similar but the Pomeroy sample is considerably smaller in mean size.

PLATE 1

Figs 1–9, 11, 14 *Lingulella ovata* M'Coy. Kildare, Grange Hill Horizon 2. **1**, BC 12634a, interior, × 2. **2**, BC 12369, exterior, × 2. **3**, BC 12635a, exterior, × 13. **4**, BC 12636, exterior, × 3. **5**, BC 12637, exterior, × 2. **6**, BC 12638, interior, × 137. **7**, BC 12634b, interior, × 2. **8**, BC 12640b, interior, × 2. **9, 11, 14,** BC 12640a, internal mould, counterpart of Fig. 8; 9, ventral view, × 2; 11, dorsal view, × 14; enlarged dorsal view showing median septum, × 2.

Fig. 12 *Schizotreta* cf. *corrugata* Cooper. Kilbride. BC 12641b, pedicle valve exterior, × 4.

Figs 10, 13 *Acanthocrania*? sp. Kildare, Grange Hill Horizon 1. Brachial valve. 10, BC 12642a, internal mould, × 10. 13, BC 12642b, external mould, × 10.

Superfamily **DISCINOIDEA** Gray, 1840
Family **DISCINIDAE** Gray, 1840
Subfamily **ORBICULOIDEINAE** Schuchert & Le Vene,
1929
Genus *SCHIZOTRETA* Kutorga, 1848

Schizotreta cf. *corrugata* Cooper, 1956   Pl. 1, fig. 12

1956   *Schizotreta corrugata* Cooper: 277; pl. 21, figs 7–20;
          pl. 28, figs 24–28.
cf. 1977   *Schizotreta* cf. *corrugata* Cooper; Mitchell: 25; pl.
          1, figs 26–30.
cf. 1984   *Schizotreta* cf. *corrugata* Cooper; Harper: 39; pl. 4,
          figs 3–5.

MATERIAL AND LOCALITY. Kilbride: a single internal and
external mould of a pedicle valve.

DESCRIPTION. Almost circular, transversely elliptical shell,
with length 95% of width. Ornament of raised concentric
ridges crowded together on either side of the umbo, number-
ing 6 per mm between 3 and 4 mm anterior of the approxi-
mate position of the umbo. Details of umbo not seen owing to
poor preservation.
   Ventral interior. Smooth, preservation too poor for detail
except faint limbus. (Dorsal valve unknown.)

MEASUREMENTS. BC 12641: (X1) length = 76 mm, (X2)
width = 8 mm (Pl. 1, fig. 12).

DISCUSSION. The size, shape and ornament suggest this is
very similar to *S. corrugata*, especially in the asymmetry of
the apex and the lateral profile of slightly concave posterior
slope and flat anterior slope. The species is recorded from
Pomeroy and Girvan although in similarly sparse numbers.

Suborder **CRANIIDINA** Waagen, 1885
Superfamily **CRANIOIDEA** Menke, 1828
Family **CRANIIDAE** Menke, 1828
Genus *ACANTHOCRANIA* Williams, 1943

Acanthocrania? sp.   Pl. 1, figs 10, 13

MATERIAL AND LOCALITY. Kildare, Grange Hill, Horizon 1:
A single internal and external mould of a brachial valve.

MEASUREMENTS. BC 12642b: X1 = 4·6 mm, X2 = 5·0 mm,
X4 = 2·3 mm (Pl. 1, fig. 13).

DISCUSSION. The preservation of this single valve, equivo-
cally assigned to *Acanthocrania*, is poor. It is steeply conical
with umbo? closer to the posterior margin. The depth is 50%
of the length, a figure close to the Portrane species *A.
cracentis* Wright, 1963, but greater than the *Acanthocrania*.

sp. of Mitchell (1977) from the Killey Bridge Formation at
Pomeroy. The internal features are not seen, but the exterior
has an impression of an oblique ribbing pattern.

Genus *ORTHISOCRANIA* Rowell, 1963

Orthisocrania divaricata (M'Coy, 1851)   Pl. 2, figs 1–8

1846   *Crania antiquissima* ? Eichwald; M'Coy: 25.
1851   *Pseudocrania divaricata* M'Coy: 187; pl. 1, H, figs 1,
          2.
1852   *Pseudocrania divaricata* M'Coy, *in* Sedgwick &
          M'Coy: pl. 1, H, figs 1, 2.
1853   *Crania divaricata* Davidson: 122; pl. 4, figs 246, 247.
1858   *Crania catenulata* (Salter MS); Baily, *in* Jukes *et al.*:
          9, fig. 3.
1859   *Crania divaricata* Salter: 212, fig. 2.
1866   *Crania* (*Pseudocrania*) *divaricata* M'Coy; Davidson:
          78; pl. 8, figs 7–12.
1875   *Crania divaricata* M'Coy; Baily: 32; pl. 11, fig. 5.
1963   *Orthisocrania divaricata* M'Coy; Rowell: 39.
cf. 1963   *Pseudocrania* cf. *divaricata* M'Coy; Williams: 345;
          pl. 1, figs 4, 5.
1965   *Orthisocrania divaricata* M'Coy; Rowell, *in* Will-
          iams *et al.*: H290, fig. 181, 6a–6c.
1970   *Orthisocrania divaricata* M'Coy; Wright: 97.
? 1976   *Orthisocrania* sp.; Neuman: 19; pl. 1, figs 1, 2.
1978   *Orthisocrania divaricata* M'Coy; Cocks: 30.
? 1980   *Orthisocrania* sp.; Lockley: 205, figs 31a, b.

MATERIAL AND LOCALITIES. Kildare, Grange Hill, Horizon
1: 41 external moulds, 10 internal moulds of brachial valves,
14 internal moulds of pedicle valves, 2 indet. internal moulds.
Kildare, Grange Hill, Horizon 2: 1 internal mould of a
pedicle valve, 3 internal moulds of brachial valves, 2 external
moulds. Carrigadaggan: 1 internal mould of a pedicle valve, 1
internal mould of a brachial valve.

DESCRIPTION. *Exterior.* Unattached, shallowly biconvex
equidimensional valves. Outline is subcircular to subquadrate
with mean length equal to width, although mean position of
maximum width (X3) is at 62% of the length from the
posterior margin. Shell is calcareous and punctate. Ornament
of fine costellae, mean value of 15 per 5 mm at 10 mm to the
anterior of the beak. Growth is mixoperipheral from mar-
ginal beak, occasionally holoperipheral in larger specimens.
Faint concentric growth lines on outer margins of larger
specimens.
   Ventral interior. The broad flat limbus is widest at the
anterior and posterior shoulders, non-pustulose and is
approximately 30% of the width. Large oval or elliptical
anterior adductor scars are slightly elevated from shell floor.

PLATE 2

Figs 1–8 *Orthisocrania divaricata* (M'Coy). Kildare, Grange Hill Horizon 1. **1**, BC 12643, latex cast of external mould, × 4. **2**, BC 12644,
   external mould, × 4. **3**, BC 12645, internal mould of brachial valve, × 2. **4**, BC 12646, internal mould of pedicle valve, × 2. **5**, BC 12647,
   internal mould of brachial valve, × 2. **6**, BC 12648, latex cast of internal mould of brachial valve, × 2. **7**, BC 12649, internal mould of
   pedicle valve, × 2. **8**, BC 12650, internal mould of pedicle valve, × 2.
Figs 9–15 *Petrocrania harperi* sp. nov. Kildare, Grange Hill Horizon 1. **9, 12**, BC 12651, external mould of brachial valve, and latex cast, both
   × 4. **10**, BC 12652, internal mould of brachial valve, × 4. **11, Holotype** BC 12653, internal mould of brachial valve, × 4. **13**, BC 12654,
   internal mould of brachial valve, × 4. **14**, BC 12655, internal mould of brachial valve, × 4. **15**, BC 12656, latex cast of external mould of
   brachial valve, × 4.
Figs 16–17 *Philhedra* sp. Kildare, Grange Hill Horizon 1. BC 12657, latex cast of external mould of brachial valve, lateral and dorsal views, ×
   2.
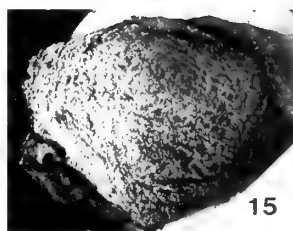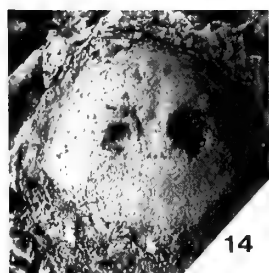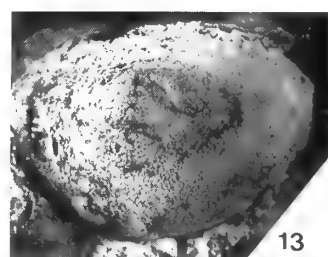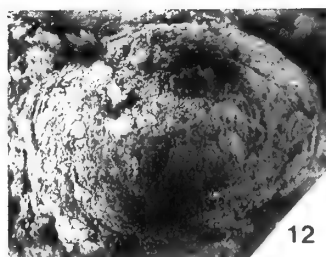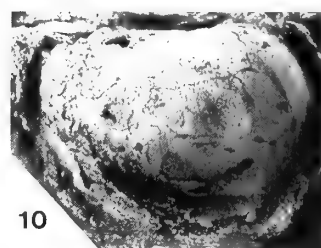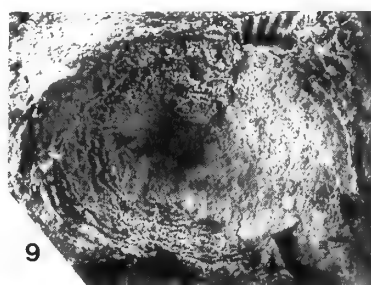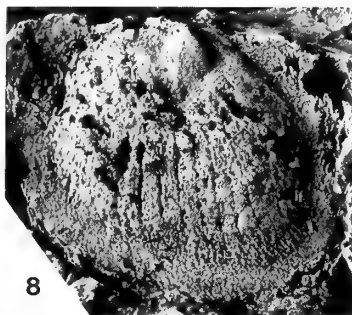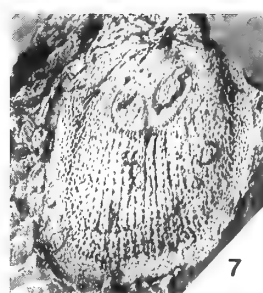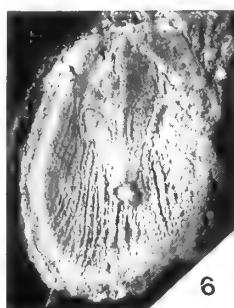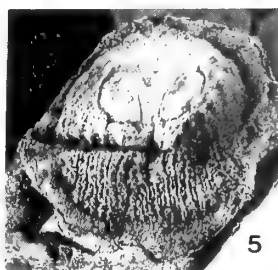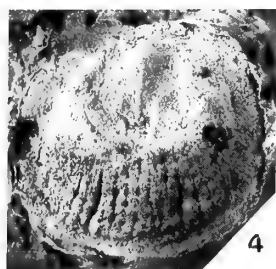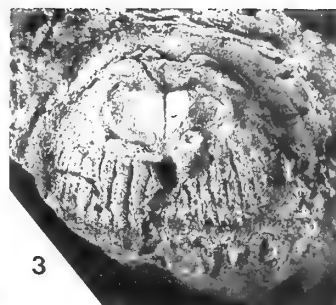
The posterior scars are smaller and less impressed. The anterior half of the shell is marked by numerous narrow ridges with broader flat interspaces, giving a very distinct pallial sinus pattern. The anterior scars are divergent from the posterior side of the mid length, towards the postero-lateral margins.

Dorsal interior. Similar in most respects to the ventral interior. Additional muscle scars on a small raised platform sagittally anterior of the anterior adductor scars.

MEASUREMENTS
External moulds:

Variates	X1	X2	X3		
Means	16·4	16·8	9·79		
Sample size	40	41	40		
Variance-covariance	14·56	8·33	8·34		
Matrix		15·0	4·38		
			6·20		

Brachial valve internal moulds:

Variates	X1	X2	X3	X8	X9
Means	16·6	17·2	10·0	2·66	8·23
Sample size	10	10	10	10	9
Variance-covariance	6·72	3·27	5·82	0·93	1·37
Matrix		6·98	4·19	0·97	−0·96
			5·76	0·91	1·06
				0·28	0·03
					1·97

Pedicle valve internal moulds:

Variates	X1	X2	X3	X8	X9
Means	17·9	17·6	11·1	2·99	8·95
Sample size	13	14	12	14	11
Variance-covariance	8·01	0·60	3·78	0·28	1·79
Matrix		9·40	0·39	0·71	0·08
			2·71	0·13	1·69
				0·19	−0.11
					1.62

DISCUSSION. Davidson (1866) provided the most complete description of this species. Although Rowell (1963) diagnosed the genus his description is sparse and no specimens are figured. The sample described herein is the first modern description of a reasonably large sample of the species with detailed morphological measurements. Rowell (1963) gave a detailed history of the complex taxonomic types, and clearly differentiated between *Orthisocrania* and the similar *Pseudocrania* on the basis of external ornament and pseudo-interareas present in the former genus. Other modern systematic records, e.g. Williams (1963), Lockley (1980) and Neuman (1976), have described only very limited or dubious material, although the preservation of Williams' (1963: 345, fig. 4; pl. 1, fig. 5) brachial valve internal mould enabled him to interpret the interior impressions better than the material described herein. This material is too inadequately preserved to be unequivocal about the presence of pseudointerareas.

In the absence of modern taxonomic references to the

Baltic species of the genus, the principal characters separating them remain unknown. Published figures (Heune 1899) and photographs (from D.A.T. Harper) of Baltic specimens show little difference, although the mean number of costellae in *O. divaricata* is apparently less than in *O. planissima*. Modern revision may show many of these species to be synonymous.

Genus *PETROCRANIA* Raymond, 1911

Petrocrania harperi sp. nov.   Pl. 2, figs 9–15

NAME. For Dr D.A.T. Harper.

DIAGNOSIS. Variably convex to conical brachial valve of oval to subcircular outline, wider than long. Posterior slope to apex concave, anterior slope convex. Apex situated at one third length from posterior margin; ornament of concentric growth lines, coarser peripherally. Dorsal interior with characteristic pair of circular anterior muscle scars between apex and mid length. Posterior scars not seen or poorly impressed. Narrow limbus sometimes developed. Ventral valve unknown.

HOLOTYPE. BC 12653 (Pl. 2, fig. 11). Paratypes BC 12651–2, BC 12654–6. Kildare Grange Hill Horizon 1.

MATERIAL AND LOCALITIES. Kildare, Grange Hill, Horizon 1: 32 internal moulds of brachial valves, 4 external moulds of brachial valves. Kildare, Grange Hill, Horizon 2: 2 internal and 4 external moulds of brachial valves.

DESCRIPTION. *Exterior*. Shallowly convex to conical brachial valves with apex situated posteriorly. Shell outline generally oval but variable from subcircular to occasionally subtriangular. Length less than width, 90% mean value, and mean depth 45% of length. Apex situated at mean value of 36% of length. Maximum width at 60% of length. Posterior slope to apex concave, occasionally flat or convex. In a few specimens the apex overhangs posterior margin. Anterior slope from apex convex, occasionally flat. Anterior profile conical to evenly convex. Ornament of concentric growth lines, variable from fine to coarse, generally coarser peripherally. Pedicle valve unknown.

Dorsal interior. Characteristic pair of circular anterior muscle scars as faint raised areas, situated at position between apex and 51% of length of shell. Smooth interior with faint posterior scars occasionally seen. Some moulds have a faint narrow limbus. (*Ventral interior* unknown).

MEASUREMENTS
Brachial valve internal moulds:

Variates	X1	X2	X3	X4	X9	X12
Mean	8·57	9·88	5·08	3·88	5·04	3·02
Sample size	32	32	29	32	16	30
Variance-covariance	5·92	6·26	3·88	2·35	1·01	1·93
Matrix		10·46	3·54	3·21	1·17	1·89
			3·09	1·58	0·37	1·32
				2·42	0·0	1·02
					1·10	0·48
						1.60

DISCUSSION. In spite of the variability in a moderately large sample the species is well defined, although it is only doubt-fully assigned to *Petrocrania*. This species does not possess the radial ornament characteristic of *Philhedra* (Wright 1963), neither does it have the spinose ornament of *Acanthocrania*, although craniid taxonomy is in need of revision. Since the status of *Philhedrella* is in some doubt (Wright 1963; Harper, 1989 personal communication) this material is assigned to *Petrocrania* on the basis of the external ornament. This is in spite of its apparently larger anterior adductor scars, supposedly a characteristic of *Philhedrella* (Wright 1963), and although the reverse is considered an important feature of *Petrocrania*. However, the material described here may simply have poorly impressed posterior scars, or even be relatively juvenile specimens of a large species for the genus. The internal morphology does not show much similarity to any described species. It resembles *Petrocrania dubia* Williams (1974), from the Soudleyan Whittery Shales in the Shelve district of Shropshire, in having (probably) larger anterior adductor scars, but differs in the apex being situated posteriorly rather than medially. Pedicle valves were not found in this sample.

Genus *PHILHEDRA* Koken, 1889

Philhedra sp.   Pl. 2, figs 16, 17

MATERIAL AND LOCALITY. Kildare, Grange Hill, Horizon 1: a single external mould of a brachial valve.

DESCRIPTION. *Exterior*. Irregularly conical subcircular convex valve, slightly asymmetrical apex. Ornament of irregular radial ribs, from apex to margins of valve. (*Interior* unknown.)

MEASUREMENTS. BC 12657: (X4) depth = 9 mm, (X2) max. diameter = 124 mm (Pl. 2, figs 16, 17).

DISCUSSION. The distinctive radial ornament is sufficient to distinguish this from the similar *Petrocrania* sp. found in abundance at the same locality, which has an ornament concentric to the apex. It also separates it from *Philhedrella*, which is very similar internally to *Philhedra* and *Petrocrania* but has no radial ornament. Although no interiors are positively assigned to *Philhedra*, there is a possibility that some of the specimens counted as *Petrocrania* in the total counts at Kildare may in fact belong to *Philhedra* sp. However, the distinctions between the genera are complicated by the inadequately known type species, discussed by Wright (1963: 251). Pending a future revision of the three craniid genera, the specimen is best assigned to *Philhedra*. Wright (1970) recorded neither *Petrocrania* nor *Philhedra* from Kildare.

Class **ARTICULATA** Huxley, 1869
Order **ORTHIDA** Schuchert & Cooper, 1932
Superfamily **ORTHOIDEA** Woodward, 1852
Family **ORTHIDAE** Woodward, 1852
Subfamily **ORTHINAE** Woodward, 1852
Genus *ORTHAMBONITES* Pander, 1830

'Orthambonites' spp.   Pl. 3, figs 1–5

MATERIAL AND LOCALITIES. Kildare, Grange Hill, Horizon 1: 6 internal moulds of brachial valves, 2 internal moulds and 2 external moulds of pedicle valves, both incomplete. Kilbride: 8 internal and 1 external moulds of pedicle valves, 14 internal and 3 external moulds of brachial valves.

MEASUREMENTS (mm)

	X1	X2
Pl.3, fig. 1.	10·5	12·6
Pl.3, fig. 2	4·0	4·6
Pl.3, figs 3, 4	6·6	9·0
Pl.3, fig. 5	5·2	7·3

DISCUSSION. The small samples are inadequate to justify assignment to any species and in any case the taxonomy of *'Orthambonites'* is in need of revision.

Subfamily **PRODUCTORTHINAE** Schuchert & Cooper, 1931
Genus *NICOLELLA* Reed, 1917

Nicolella cf. *actoniae* (J. de C. Sowerby, 1839)
                                                   Pl. 3, figs 6–9, 11

MATERIAL AND LOCALITIES. Kilbride: 10 internal and 8 external moulds of pedicle valves, 6 external moulds of brachial valves; all material is fragmentary. Carrigadaggan: 3 internal and 8 external moulds of pedicle valves, 1 internal and 5 external moulds of brachial valves; material is mostly fragmentary. Greenville-Moyne: 3 internal and 7 external moulds of brachial valves, 3 internal and 4 external moulds of pedicle valves and 1 conjoined internal mould. Kildare, Grange Hill, Horizon 1: 1 internal and 1 external mould of a brachial valve.

DISCUSSION. Williams (1974: 58) commented on the morphological stability of *Nicolella actoniae* from mid Caradoc to early Ashgill times. All the samples here are probably very close to *N. actoniae*, or the subspecies *N. actoniae obesa* Williams (1963) from Bala, North Wales, a much deeper form than the nominate subspecies. All the samples collected here are poorly preserved and mostly broken, as well as relatively small in numbers; hence measurements of variation and counts of rib numbers are not possible. Thus assignment to one species, or several, is unrealistic until larger samples are available to assess the variation in morphology.

The Greenville-Moyne sample is apparently not as deep in the ventral valve as that from Carrigadaggan or Kilbride, but this may be a preservational effect, owing to disparity in compaction between the fine-grained mudstones of Greenville-Moyne, and the coarse volcaniclastics of Carrigadaggan or the tuffaceous siltstones of Kilbride. The latter
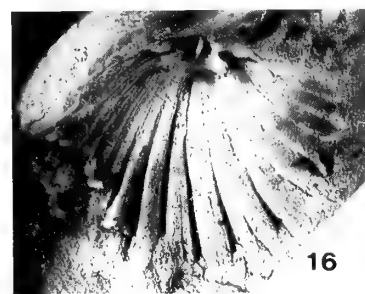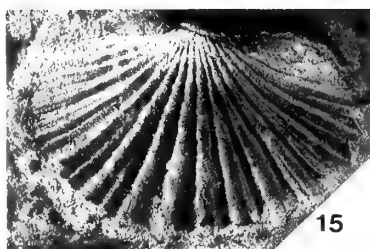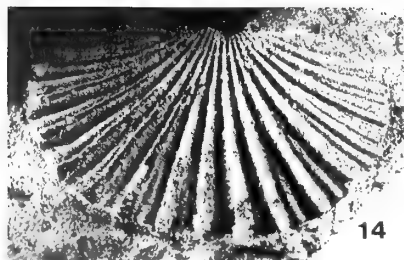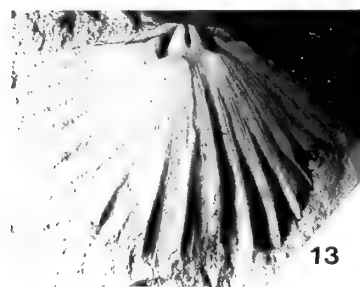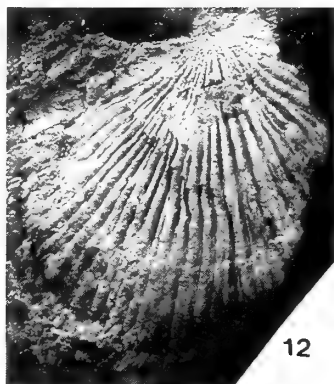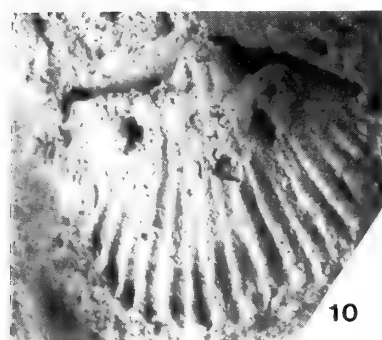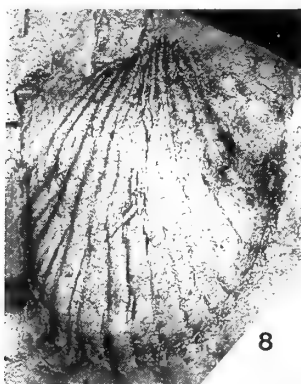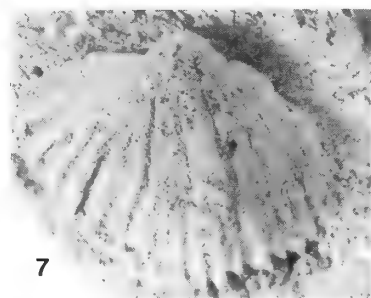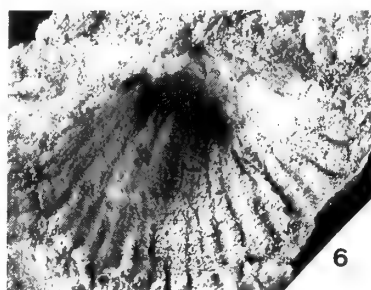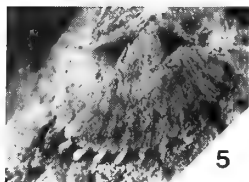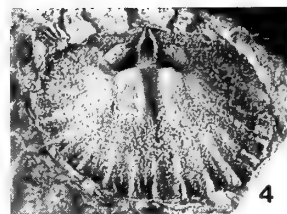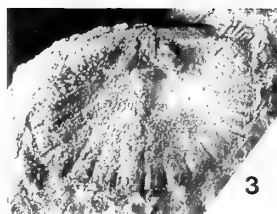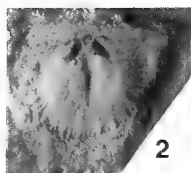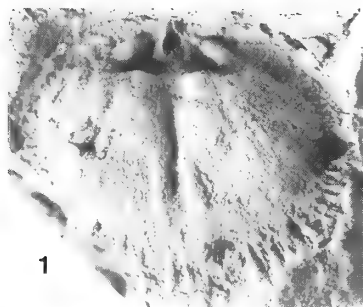
two samples are strongly convex in the pedicle valve and appear most similar to *N. actoniae obesa*, from the Gelli-grin Formation of the Bala district. The broken nature of the samples, particularly of the Kilbride one (as are most species from there), generally precluded counts of rib numbers, but three brachial valve external moulds from Kilbride had 10, 12 and 15 ribs, and one pedicle valve had 11 in total.

Type specimens of *N. interplicata* (M'Coy, 1846), from the Kildare Limestone Formation, were examined (NMI-lectotype F4565, paralectotypes F5564 and F11604), but they are inadequate for formal comparison. Indeed the latter specimen is probably not a *Nicolella* at all. As noted by Cocks (1978) the evaluation of topotypes from the Kildare Limestone Formation is necessary to assess this species. Whether *Nicolella calcarata* M'Coy (1846), cited as rare in the slates of Greenville and very common in the slates of Slieveroe, Rathdrum, is simply a deformed version of *N.* cf. *actoniae* or a separate species is not clear, since no Greenville topotypes were recovered. The lectotype (F4567) is broken and did not appear similar to any of the samples, being more transverse and coarsely costate. A paralectotype (F5509) from Slieveroe is also deformed and broken but appears similar to *N.* cf. *actoniae*.

Larger collections of better-preserved material would be desirable to enable both a biometric comparison with *N.* cf. *actoniae* and described subspecies as well as pre-Longvillian species such as *N. humilis* (Whittington & Williams 1955) and *N.* cf. *strasburgensis* (Williams 1962). Provisionally, the present material is compared to *N. actoniae* which, as presently understood, encompasses a wide range of variation and a lengthy time span (mid Caradoc – mid Ashgill).

Nicolella ? sp.   Pl. 3, fig. 12

MATERIAL AND LOCALITY. Kilbride: 1 internal and external mould of a brachial valve.

DISCUSSION. This single concave brachial valve is questionably assigned to *Nicolella*, but is different from the other samples of the genus, including the Kilbride material, principally in being large and having a much greater ribbing frequency (at least 26 ribs). The brachial interior has the erect cardinal process, short divergent brachiophores and heavy deposits of secondary shell ankylosing the brachiophores to a short median ridge which are characteristic of *Nicolella*. It may possibly be compared to *N. asteroidea* Reed, which has more ribs than *N. actoniae*, but the preservation of the specimen is inadequate to assess the branching pattern of costellae.

Family **DOLERORTHIDAE** Öpik, 1934
Subfamily **HESPERORTHINAE** Schuchert & Cooper, 1931
Genus ***HESPERORTHIS*** Schuchert & Cooper, 1931

Hesperorthis sp.   Pl. 3, fig. 10

MATERIAL AND LOCALITY. Kilbride: 3 internal moulds of pedicle valves.

DISCUSSION. The small numbers of the genus are inadequate for specific determination, but the long apsacline interarea and overall shape suggest the specimens belong to *Hesperorthis*. The genus is known from the Caradoc rocks of Grangegeeth, as the Estonian species *H. inostranzefi*, but the Kilbride species is dissimilar and much smaller. Two species are known from Girvan (Williams 1962) and one from the Llanvirn of Wales (Lockley & Williams 1981), but formal comparison requires a better preserved and larger sample from Kilbride.

Family **PLAESIOMIIDAE** Schuchert, 1913
Subfamily **PLAESIOMIINAE** Schuchert, 1913
Genus ***PLAESIOMYS*** Hall & Clarke, 1892

Plaesiomys multiplicata Bancroft, 1945
           Pl. 3, figs 13–16; Pl. 4, figs 1–6; Pl. 7, fig. 12

? 1896   *Orthis flabellulum* Sowerby; Reynolds & Gardiner: 589.
1945   *Dinorthis* (*Plaesiomys*) *multiplicata* Bancroft: 244; pl. 35, figs 4–6; pl. 36, figs 1–3.
1968   *Dinorthis multiplicata* Bancroft; Diggens & Romano: 47; pl. 5, fig. M.
1978   *Plaesiomys multifida* (Salter); Cocks: 50 (*pars*).
1978   *Dinorthis multiplicata* Bancroft; Brenchley: 160.
1980b *Lordorthis* sp.; Mitchell, *in* Romano: 206.
cf. 1985 *Plaesiomys* cf. *multiplicata* Bancroft; Harper *et al.*: 291; figs 6–24.

MATERIAL AND LOCALITY. Kildare, Grange Hill House Cottage: 26 internal and 12 external moulds of pedicle valves; 13 internal and 20 external moulds of brachial valves.

DESCRIPTION. *Exterior.* Large, dorsibiconvex to convexiplane valves of rounded subquadrate outline, with maximum width just anterior of hinge line, and about two-thirds as long as wide. Evenly convex anterior and lateral profiles in brachial valve, but pedicle valve flat to weakly concave except for swollen posterior axial surface. Ventral interarea flat and apsacline with open delthyrium. Dorsal interarea flat and orthocline, with open notothyrium. Radial ornament of evenly rounded costae and costellae and interspaces, and

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PLATE 3

Figs 1–5 'Orthambonites' spp. **1, 3–4** Kildare, Grange Hill Horizon 1. **1**, BC 12658, internal mould of brachial valve, × 4. **3, 4**, BC 12660, internal mould of brachial valve, latex cast and mould, × 4. Figs **2, 5** Kilbride. **2**, BC 12659, internal mould of brachial valve, × 4. **5**, BC 12661, internal mould of pedicle valve, × 4.

Figs 6–9, 11 Nicolella cf. actoniae (J. de C. Sowerby). **6–7, 9** Kilbride. **6, 7**, BC 12662, internal mould of pedicle valve, latex cast and mould, × 4. **9**, BC 12664a, internal mould of pedicle valve, × 2. Figs **8, 11** Greenville-Moyne. **8**, BC 12663b, external mould of pedicle valve, × 2. **11**, BC 12663a, internal mould of pedicle valve, counterpart of Fig. 8, × 2.

Fig. 10 Hesperorthis sp. Kilbride. BC 12666, internal mould of pedicle valve, × 10.

Fig. 12 Nicolella? sp. Kilbride. BC 12665b, external mould of brachial valve, × 2.

Figs 13–16 Plaesiomys multiplicata Bancroft. Kildare, Grange Hill House Cottage. **13, 16**, BC 12667, internal mould of brachial valve, and latex cast, × 4. **14, 15**, BC 12668, external mould of pedicle valve, and latex cast, × 4.
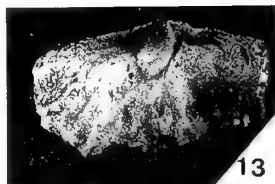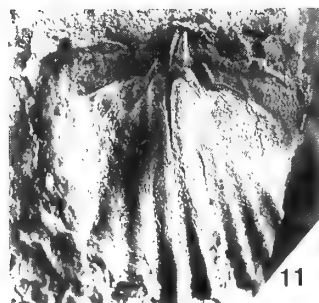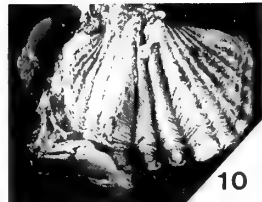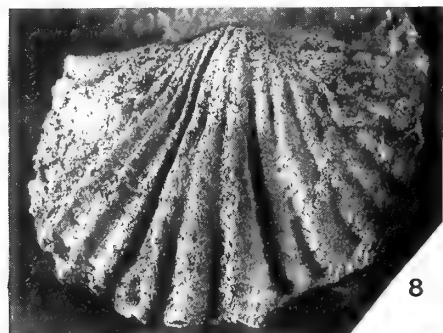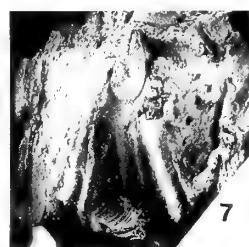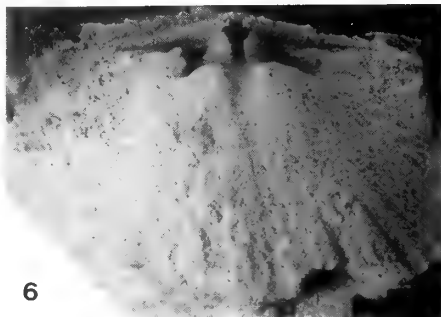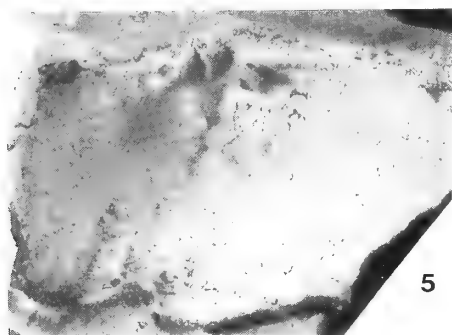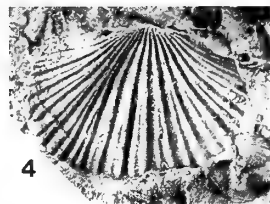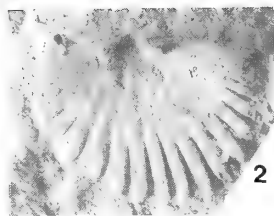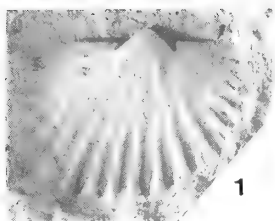
very fine concentric growth lines. Counts of 18–25 costae and costellae are present on 2, 0, 0, 1, 1,1, 0 and 1 valve exteriors at the 5 mm growth stage and counts of 27 and 31 costae and costellae on 2 and 1 valve exteriors at the 10 mm growth stage.

Ventral interior. Stout, small teeth directed dorsilaterally from anterior margins of wide delthyrium are supported by strong receding dental plates. External ornament strongly impressed, particularly near anterior margins.

Dorsal interior. Simple, linear cardinal process is slightly thickened posteriorly, situated on notothyrial platform which extends anteriorly for one-third of valve length as a low broad ridge. Blade-like, divergent brachiophores supported by stout bases which, with the hinge line, define deep sockets.

DISCUSSION. Although large, the sample cannot easily be statistically compared to the existing descriptions of the species because many of the specimens are broken or poorly preserved. However, sufficient distinctive material is described to assign it confidently to the species illustrated by Bancroft (1945) from the Soudleyan of Glyn Ceiriog, North Wales, and in particular the sample described by Harper & Mitchell (Harper *et al.*, 1985) from the Clashford House Formation of Co. Meath. Re-collection of more specimens will allow a better assessment of the variability in the species, particularly in external ornament, since the available material shows a few specimens more like the closely related genus *Dinorthis*, than like *Plaesiomys*. The relationship of these two genera is in need of reassessment. However, the record of *Orthis flabellulum* from here (Reynolds & Gardiner 1896) is probably the present species. Lamont (1953) noted that it was 'apparently a late variety of J. de C. Sowerby's species with bifurcation and trifurcation of ribs'. The specimens collected by Lamont are now held in the National Museum of Ireland, but were apparently never figured or described. They are labelled as '*Dinorthis peplos*' on Lamont's labels, but no publication of this name is known.

Family **PLECTORTHIDAE** Schuchert & Le Vene, 1929
Subfamily **PLATYSTROPHINAE** Schuchert & Le Vene, 1929
Genus *PLATYSTROPHIA* King, 1850

Platystrophia sp. 1   Pl. 4, figs 7–17; Pl. 5, figs 1–3

MATERIAL AND LOCALITIES. Kildare, Grange Hill, Horizon 1: 30 internal and 17 external moulds of pedicle valves; 33 internal and 13 external moulds of brachial valves; 6 internal and 10 external conjoined moulds; 12 external fragments. Most of the material assigned to *Platystrophia* is incomplete. Kildare, Grange Hill, Horizon 2: 1 conjoined shell and one brachial valve.

DISCUSSION. Although the large sample of specimens from Grange Hill, Kildare, was clearly identifiable as *Platystrophia* in both internal and external moulds, the material is almost all fragmentary or partially broken, precluding valid measurements. A statistical assessment was not possible. Since *Platystrophia* is a ubiquitous genus in Middle and Upper Ordovician rocks in Europe and America, with little variation amongst the many described species, it is necessary to reiterate the need for a complete species revision. Many authors such as Williams (1962: 126; 1963: 371), Wright (1964: 206), Cocks (1978: 55) and Hiller (1980: 143) have discussed the artificial nature of Cumings' (1903) scheme of species groupings, elaborated further by McEwan (1920) and modified in terminology by Schuchert & Cooper (1932: 67). In this scheme, the present material is all placed in the bicostate group, with 2 costae in the ventral sulcus and 3 on the dorsal fold. The counts on suitable material showed there were 1, 5, 3 and 2 pedicle valves with 4, 5, 6 and 7 costae respectively, on each flank.

The Kildare population is finely pustulose, but distinguishing it from other species is a concentric ornamentation inviting comparisons with *P. caelata* Williams from the Soudleyan of Shelve, Shropshire (Williams 1974: 76–77; pl. 12, figs 13, 14, 16–19). The ornament is of differentially developed lamellae, but further investigation would be needed to assess whether the lamellae are of the distinctive *P. caelata* type or merely accentuated growth lines. In his description Williams stated that *P. caelata* is uniplicate, but later noted all specimens are biplicate (bicostate); this would appear to be correct from the figures.

Platystrophia sp. 2   Pl. 5, figs 4, 5

MATERIAL AND LOCALITY. Kilbride: 1 external and 3 internal moulds of brachial valves; 1 internal and 1 external moulds of pedicle valves, all incomplete.

DISCUSSION. The present material is inadequate for specific determination but appears to differ from *Platystrophia* sp. 1 from Kildare, Grange Hill in having 7 ribs on the ventral flanks, although being of smaller average size. It also lacks the strongly developed overlapping lamellae, although in other respects it is similar, belonging to the bicostate group.

Subfamily **RHACTORTHINAE** Williams, 1963
Genus *RHACTORTHIS* Williams, 1963

Rhactorthis sp.   Pl. 5, figs 6–11

MATERIAL AND LOCALITY. Kildare, Grange Hill, Horizon 1: 4 internal and 2 external moulds of brachial valves, 2 external moulds of pedicle valves and 1 conjoined internal and external mould.

PLATE 4

Figs 1–6 *Plaesiomys multiplicata* Bancroft. Kildare, Grange Hill House Cottage. **1, 2,** BC 12669, internal mould of pedicle valve, and latex cast, × 4. **3, 4** BC 12670, external mould of brachial valve, latex cast and mould, × 2. See also Pl. 7, fig. 12. **5, 6,** BC 12671, internal mould of brachial valve, latex cast and mould, × 4.

Figs 7–17 *Platystrophia* sp. 1. Kildare, Grange Hill Horizon 1. **7,** BC 12672, internal mould of pedicle valve, × 2. **8,** BC 12673, latex cast of external mould of brachial valve, × 4. **9,** BC 12674, latex cast of external mould of pedicle valve, × 4. **10,** BC 12675, latex cast of external mould of pedicle valve, × 2. See also Pl. 5, fig. 2. **11, 17,** BC 12676, internal mould and latex cast of brachial valve, × 4. **12, 15,** BC 12677, external mould and latex cast of brachial valve, × 4. See also Pl. 5, fig. 1. **13,** BC 12678a, internal mould of pedicle valve, × 2. **14,** BC 12679, latex cast of external mould of brachial valve, with a *Petrocrania* attached, × 2. **16,** BC 12680a, internal mould of brachial valve, × 4.

MEASUREMENTS (mm)

	X1	X2	X3	
Pl.5, figs 8,9	8·1	10·4	3·1	(conjoined internal mould)
Pl.5, fig.10	8·2	11·1	4·1	(brachial valve)
Pl.5, figs 6,11	9·8	9·5	–	(strained brachial valve)

DISCUSSION. The sparse numbers of this genus from Kildare are inadequate to justify assignment, either to the type species *R. crassa* Williams from the Longvillian of Bala, or to either of the other Caradoc species *actoniae* and *grandis* erected by Hurst (1979a), from the type Caradoc of Shropshire. Its presence, however, serves to emphasize the similarities of the Kildare fauna to that of the Bala district of North Wales.

Family **CREMNORTHIDAE** Williams, 1963
Subfamily **CREMNORTHIDAE** Williams, 1963
Genus ***CREMNORTHIS*** Williams, 1963

Cremnorthis parva Williams, 1963
Pl. 5, figs 12–16; Pl. 6, figs 1–7
1963 *Cremnorthis parva* Williams: 379; pl. 4, figs 15–23; text-fig. 9.

MATERIAL AND LOCALITIES. Kildare, Grange Hill, Horizon 1: 38 internal moulds of brachial valves, 31 internal moulds of pedicle valves; 14 external moulds of brachial valves, 7 external moulds of pedicle valves. Carrigadaggan: 3 internal and 1 external moulds of pedicle valves, 3 internal moulds of brachial valves. Kilbride: 9 internal and 1 external moulds of pedicle valves, 6 internal moulds of brachial valves. Greenville-Moyne: 8 internal moulds of pedicle valves and 2 internal moulds of brachial valves.

DESCRIPTION. *Exterior.* Subcircular to semicular outline, moderately biconvex, with both valves about three-tenths as deep as long. Maximum width occurring at less than one-third the length of the shell. Length of brachial valve about seven-tenths of the width. Pedicle valve length about four-fifths of width. Brachial valve gently sulcate, with flatly convex lateral profile. Dorsal interarea short and anacline, ventral interarea apsacline and about a quarter the length of the valve. Radial ornamentation costellate with angular costae and costellae about 5 per mm at 2 mm anterior of umbones. Shell impunctate.
Ventral interior. Short teeth connected to shell floor by

thickened deposits, and long apsacline interarea, which together bound a deep umbonal cavity. Subtriangular muscle scar does not extend much beyond cavity anteriorly. Muscle field composed of wide median adductor scars flanked by pair of narrow diductor scars which are lobate anteriorly. Sagittal length of muscle field nearly two-fifths length of valve.
Dorsal interior. Large cardinal process, standing above hinge line, is continuous with blade-like median septum which extends four-fifths of the valve length, and is highest at about mid-length. Brachiophores short and slightly divergent, continuous with bases which curve posterolaterally as fulcral plates to define subtriangular sockets. Brachiophore bases are situated at about a quarter of the valve length.

MEASUREMENTS
Pedicle valve internal moulds (Kildare, Horizon 1):

Variates	X1	X2	X3	X4	X5	X6	X9	X10
Means	3·31	3·39	1·22	0·96	2·84	0·96	1·33	1·08
Sample size	29	30	30	29	19	19	26	25
Variance-covariance	0·50	0·39	0·21	0·10	0·23	0·04	0·20	0·14
Matrix		0·57	0·14	0·08	0·36	0·04	0·14	0·14
			0·18	0·05	0·09	0·03	0·13	0·08
				0·05	0·06	0·01	0·04	0·03
					0·39	0·03	0·08	0·08
						0·02	0·03	0·02
							0·14	0·08
								0·07

Brachial valve internal moulds (Kildare, Horizon 1):

Variates	X1	X2	X3	X4	X17	X18	X24
Means	3·07	3·44	1·13	0·87	0·77	1·28	2·54
Sample size	38	37	36	35	35	35	38
Variance-covariance	0·46	0·38	0·14	0·08	0·08	0·10	0·33
Matrix		0·76	0·09	0·10	0·08	0·15	0·26
			0·10	0·01	0·03	0·02	0·01
				0·04	0·01	0·03	0·06
					0·03	0·03	0·06
						0·06	0·08
							0.30

DISCUSSION. The numerical data in the description are based only on the mean values for the large sample from Grange Hill, Kildare, where this species is a very common element of the fauna. The poor preservation of the samples from Kil-

Fig. 16 Palaeogeographic reconstruction of the Iapetus region in mid-Caradoc times (*c.* 448 Ma) showing the main continental masses of Laurentia, Baltica, Gondwana and Eastern and Western Avalonia. The main brachiopod provinces of Scoto-Appalachian, Baltic and Mediterranean affinity are also shown. At this time, an Anglo-Welsh Province, including these Leinster faunas, was centred on Eastern Avalonia (after Parkes, 1992).

bride and Carrigadaggan made measurement of all variates difficult, but a principal component analysis (PCA) of all three samples shows that in plots of the first four eigenvectors (see Fig. 17) the two small samples fall within the same region as the Kildare sample. It is possible that analysis of a larger topotype sample of the species would show significant differences between the Welsh and Irish forms, but the original description was based on fewer than ten valves. The mean percentage length of the ventral muscle field relative to the valve length is significantly longer in the Irish form (Kildare – 39% compared to 35%, p < 0·01). This is considered inadequate to justify erection of even a new subspecies, since the Bala sample consisted of only 5 specimens. A larger, better preserved sample would probably encompass the same variation seen in the Kildare form.

PLATE 6

Figs 1–7 *Cremnorthis parva* Williams. **Figs 1–5**, Kildare, Grange Hill Horizon 1. **1**, BC 12689, internal mould of brachial valve, × 5. **2, 3**, BC 12690, internal mould of pedicle valve, latex cast and mould, × 15. **4**, BC 12691, internal mould of brachial valve, and BC 12692, internal mould of pedicle valve, both × 6. **5**, BC 12693, internal mould of brachial valve, × 3. **Figs 6, 7**, Carrigadaggan. **6**, BC 12694, ventral view of conjoined internal mould, × 10. **7**, BC 12695, internal mould of pedicle valve, × 10.

Figs 8–16 *Skenidioides costatus* Cooper. Kildare, Grange Hill Horizon 1. **8, 12**, BC 12696, dorsal and ventral views of conjoined internal mould, × 10. **9**, BC 12697, internal mould of brachial valve, × 10. **10**, BC 12698, internal mould of brachial valve, × 10. **11**, BC 12699, ventral view of conjoined internal mould, × 10. **13**, BC 12700, internal mould of pedicle valve, × 10. **14**, BC 12701, internal mould of pedicle valve, × 10. **15**, BC 12702, internal mould of pedicle valve, × 10. **16**, BC 12703, internal mould of pedicle valve, × 10.
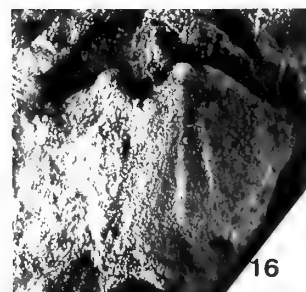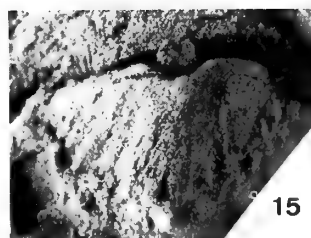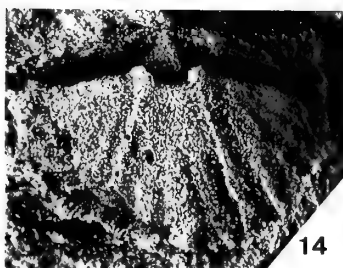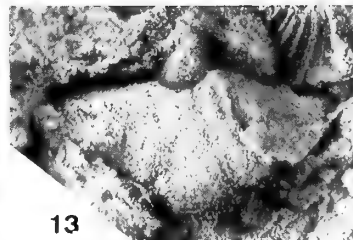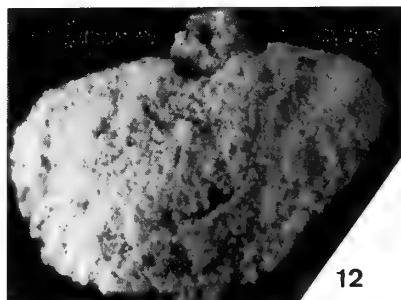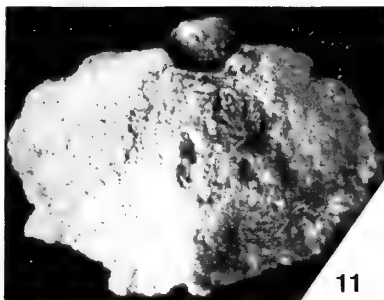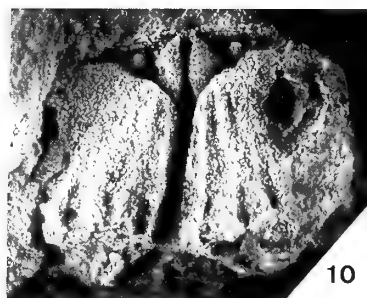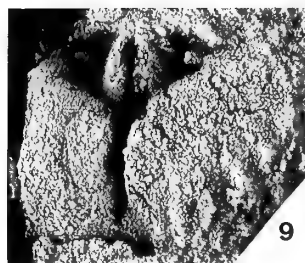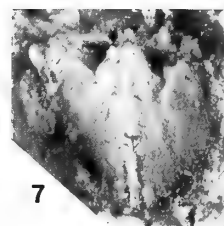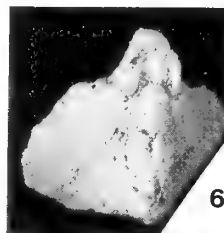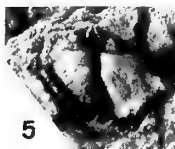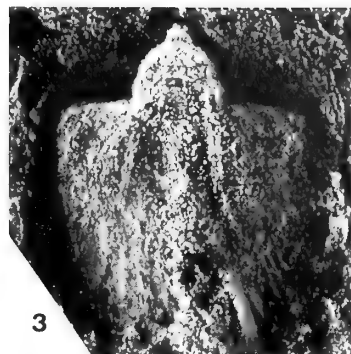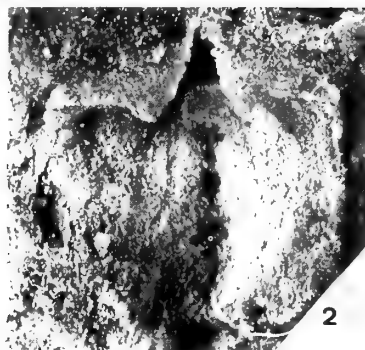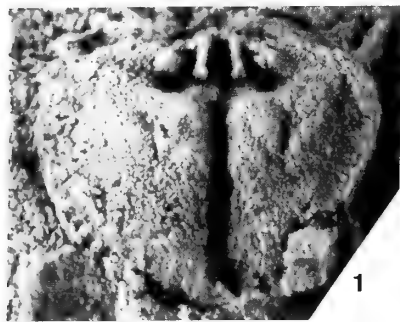
Family **SKENIDIIDAE** Kozlowski, 1929
Genus *SKENIDIOIDES* Schuchert & Cooper, 1931

Skenidioides costatus Cooper, 1956

Pl. 6, figs 8–16; Pl. 7, figs 1–5
1956   *Skenidioides costatus* Cooper: 493; pl. 97, figs
        38–48.
aff. 1962   *Skenidioides* aff. *costatus* Cooper; Williams: 126;
        pl. 11, figs 24–27, 52.
cf. 1963   *Skenidioides* cf. *costatus* Cooper; Williams:
        375–377; pl. 4, figs 7–14.
cf. 1974   *Skenidioides* cf. *costatus* Cooper; Williams:
        82–83; pl. 13, figs 14–16; pl. 14, figs 1–3.
cf. 1979a   *Skenidioides* cf. *costatus* Cooper; Hurst: 242; figs
        145–159.

MATERIAL AND LOCALITIES. Kilbride: 2 internal and 3 external moulds of pedicle valves; 3 internal and 6 external moulds of brachial valves. Kildare, Grange Hill, Horizon 1: 10 internal and 10 external moulds of brachial valves; 19 internal and 3 external moulds of pedicle valves. Kildare,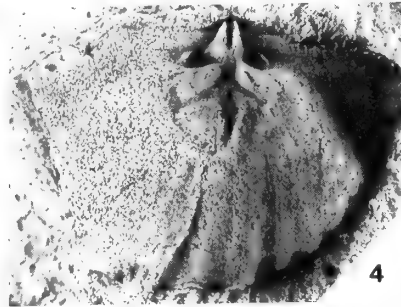 Grange Hill House Cottage: 2 internal and 1 external moulds of pedicle valves; 1 internal and 2 external moulds of brachial valves. Carrigadaggan: 1 internal mould of a pedicle valve. Kildare, Grange Hill, Horizon 2: 3 internal moulds of pedicle valves. Greenville-Moyne: 1 internal and 1 external moulds of a pedicle valve.

DESCRIPTION. *Exterior*. Ventribiconvex, subpyramidal *Skenidioides* with pedicle valve length about seven-tenths of the length, and about 40% as deep as long. Brachial valve gently convex with distinct median sulcus, about 50–70% as long as wide. Ornament of radial costellae, about 2–5, commonly 3, ribs per mm 2mm anteromedially of umbo, in both valves. Commonly a wider median rib on the pedicle valve, with total rib counts of between 12 and 20 with 15–17 the most common frequency. Ventral interarea high, catacline to apsacline with open delthyrium. Dorsal interarea shorter, anacline.

Ventral interior. Generally unsupported spondylium about a quarter as long as the valve, and about 94% as long as wide. Some shells have a median thickened ridge of shell supporting the spondylium.

Dorsal interior. Thin median septum, continuous anteriorly from shaft-like cardinal process, extending about 90% of valve length. Slender brachiophores with bases convergent onto median septum defining a diamond shaped cruralium about a third as long as valve.

DISCUSSION. Previously described samples compared to *S. costatus* (Cooper 1956) differ in some proportions from each other and from the material described here, but the differences are not considered important enough to warrant taxonomic recognition. Principal component analysis of all the

MEASUREMENTS
Pedicle valve internal moulds (Kildare, Horizon 1):

Variates	X1	X2	X4	X13	X14
Means	3·37	4·64	1·29	0·81	0·84
Sample size	19	19	19	18	18
Variance-covariance	0·46	0·42	0·06	0·13	0·06
Matrix		0·77	0·05	0·10	0·08
			0·08	0·01	0·01
				0·06	0·03
					0·02

Brachial valve internal moulds:

Variates	X1	X2	X15	X16	X24
Means	3·00	4·11	0·98	0·83	2·76
Sample size	10	10	10	10	10
Variance-covariance	0·25	0·24	0·06	0·02	0·26
Matrix		0·78	0·02	0·10	0·14
			0·03	0·0	0·06
				0·02	0·0
					0·32

Brachial valve external moulds:

Variates	X1	X2	X4
Means	2·73	5·32	0·47
Sample size	10	10	7
Variance-covariance	0·43	0·63	0·05
Matrix		1·17	0·14
			0·12

material shows no differentiation on the first four vectors, as shown in Fig. 18. As noted by Mitchell (1977: 50) and Hiller (1980: 146), internal features of many *Skenidioides* species show no significant differences, the species being separated on the basis of the density of external ornament. The rib counts for this Irish material is comparable to previously described populations of *S. costatus* of similar size range.

One aspect which apparently requires further investigation is the branching mode of the ribs of the species. Williams (1974: 83) discussed the differences between Shelve and Bala stocks, with new costellae arising only from the ventral median rib in the former and branching freely from lateral costae in the latter. In the Bala stocks, the majority of costae branched externally (Williams 1963: 377). However, Hurst (1979a: 242) states that the Shropshire stock only branched

PLATE 7

Figs 1–5 *Skenidioides costatus* Cooper. Kildare, Grange Hill Horizon 1. **1, 3**, BC 12704, external mould of brachial valve and interareas, × 6, and enlarged oblique posterior view of latex cast of interareas, showing hinge line and open delthyrium and notothyrium, × 10. **2**, BC 12809, latex cast of external mould of pedicle valve, × 6. **4, 5**, BC 12705, external mould of brachial valve and interareas, and latex cast showing open delthyrium, × 10.

Figs 6–11 *Oanduporella* cf. *reticulata* Hints. Kildare, Grange Hill House Cottage. **6, 9**, BC 12706, external mould of pedicle valve, latex cast and mould, × 10. **7, 8**, BC 12707a (upper) and BC 12708a (lower); internal moulds and latex cast of 2 pedicle valves, × 4. **10**, BC 12711b, external mould of pedicle valve, × 4. **11**, BC 12711a, internal mould of pedicle valve, counterpart of Fig. 10, × 4.

Fig. 12 View of slab, containing BC 12670, external mould of *Plaesiomys multiplicata* Bancroft (P; see also Pl. 4, figs 3–4), to illustrate the typical assemblage at Kildare, Grange Hill House Cottage; with *Oanduporella* cf. *reticulata* Hints (A), *Rafinesquina* sp. (B), and numerically dominant gastropods (C). × 1.
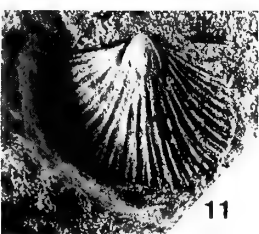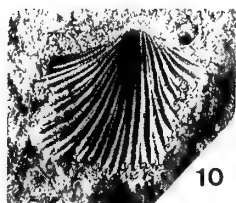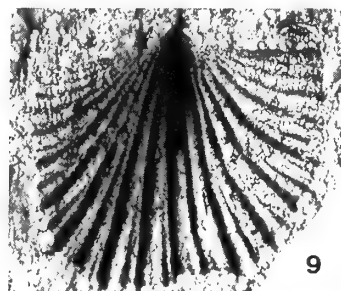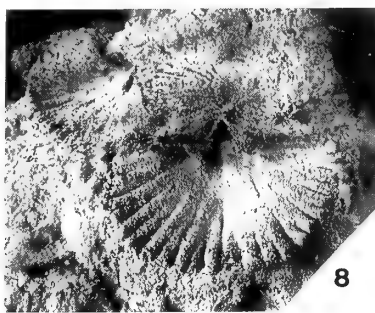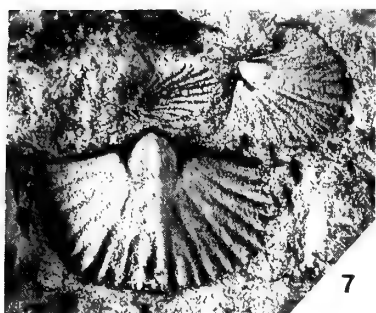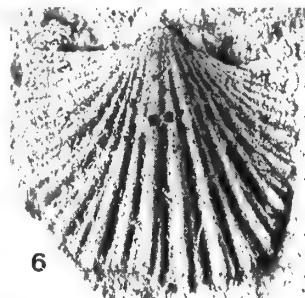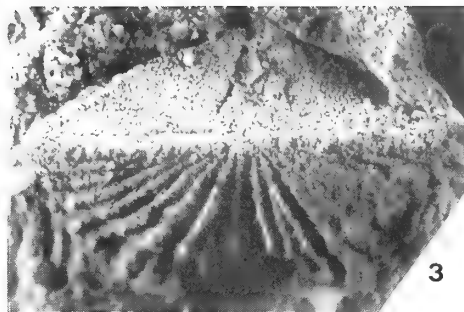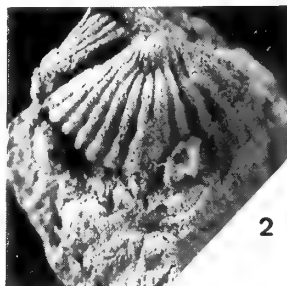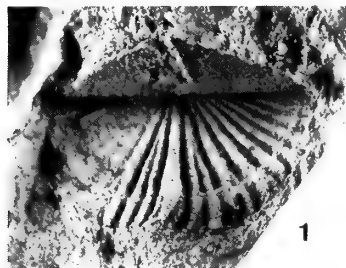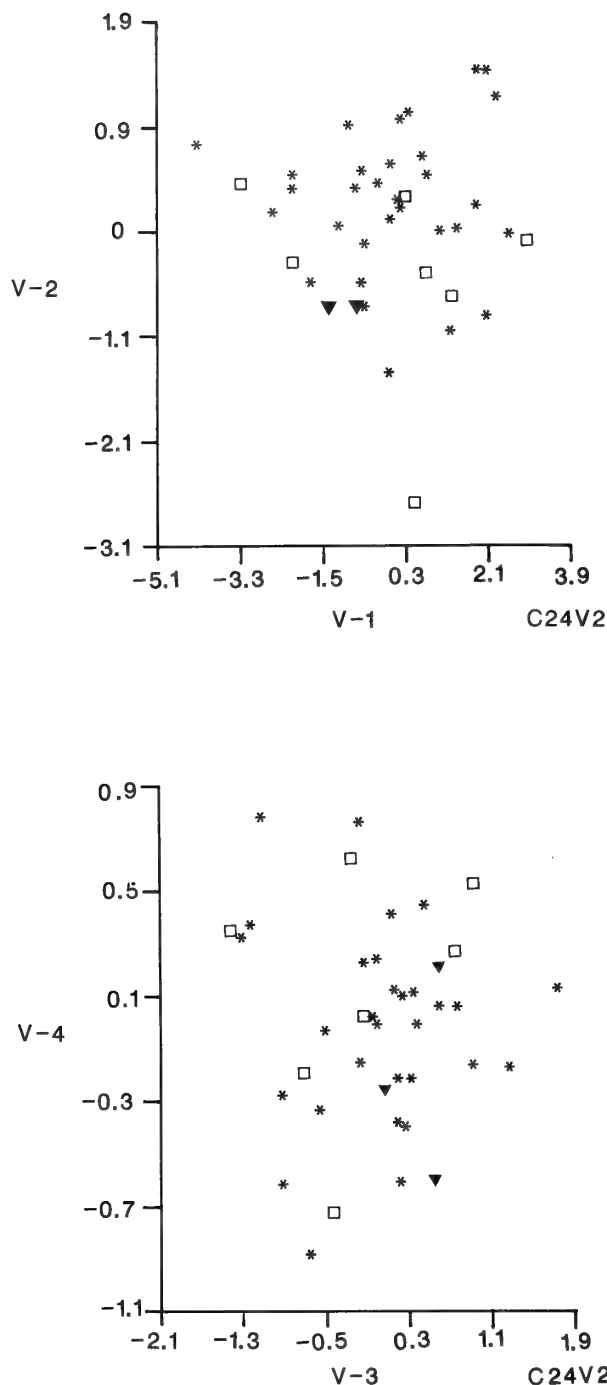
Fig. 17 Principal component analysis of samples of *Cremnorthis parva*, internal moulds of pedicle valves only. Top, vector 1 against vector 2. Below, vector 3 against vector 4. ▼ = Carrigadaggan, * = Kilbride, □ = Kildare, Grange Hill Horizon 1.

internally. The present material has few external moulds with costellae, but those that do, show both internal and external branching.

Superfamily **ENTELETOIDEA** Waagen, 1884
Family **DALMANELLIDAE** Schuchert, 1913
Genus *OANDUPORELLA* Hints, 1975

Oanduporella cf. *reticulata* Hints, 1975

Pl. 7, figs 6–12; Pl. 8, figs 1–7

cf. 1975 *Oanduporella reticulata* Hints: 19, 105; pl. 1, figs 1–15; pl. 2, figs 1–5.
1980a? *Ravozetina/Onnizetina*; Mitchell, *in* Romano: 206.
1985 *Oanduporella* cf. *reticulata* Hints; Harper & Mitchell, *in* Harper *et al.*: 295, figs 25–37.

MATERIAL AND LOCALITY. Kildare, Grange Hill House Cottage: 10 internal and 6 external moulds of brachial valves, 13 internal and 9 external moulds of pedicle valves.

DISCUSSION. Harper & Mitchell gave a full description (Harper *et al.*, 1985) of material they compared to Hints' species from the east Baltic, with which the present material from Kildare accords well. The Herbertstown material, from the Clashford House Formation, was the first record of the genus from Britain or Ireland and the present sample represents the second known occurrence from these areas. It serves to emphasize the similarities of the Kildare fauna to that from Herbertstown with two conspecific forms, *Plaesiomys multiplicata* Bancroft and *Oanduporella* cf. *reticulata* Hints, present, with a possible third, *Hibernodonta*? Harper & Mitchell (*in* Harper *et al.* 1985). There are few suitable specimens but similar rib counts (5–6 per 2 mm at 5 mm sagittally) are seen in the Kildare specimens, although the microsculpture is well developed on most specimens.

Oanduporella sp. (Not figured)

MATERIAL AND LOCALITY. Greenville: 3 external and 1 internal moulds of pedicle valves, 1 external mould of a brachial valve.

DISCUSSION. The poor preservation, and deformation in this mudstone lithology made it impossible to compare this material to the specimens from Kildare, Grange Hill House Cottage. Nevertheless, this small sample shows the characteristic pitted microsculpture of the genus and extends the known geographical range.

Genus *REUSCHELLA* Bancroft, 1928

Reuschella ? sp. Pl. 11, fig. 16

MATERIAL AND LOCALITY. Kilbride: A single internal mould of a pedicle valve.

DISCUSSION. The single poorly preserved mould is assigned to *Reuschella* on the basis of the sharp median carina, curved long apsacline interarea, the ventral muscle scar and massive teeth. The specimen represents the sole occurrence of the genus within the southeast Ireland Caradoc. It is known from the Actonian of Shropshire (Hurst 1979a), the Soudleyan of Shelve, Shropshire (Williams 1974) and Bala (Williams 1963) as well as from Girvan (Williams 1962).
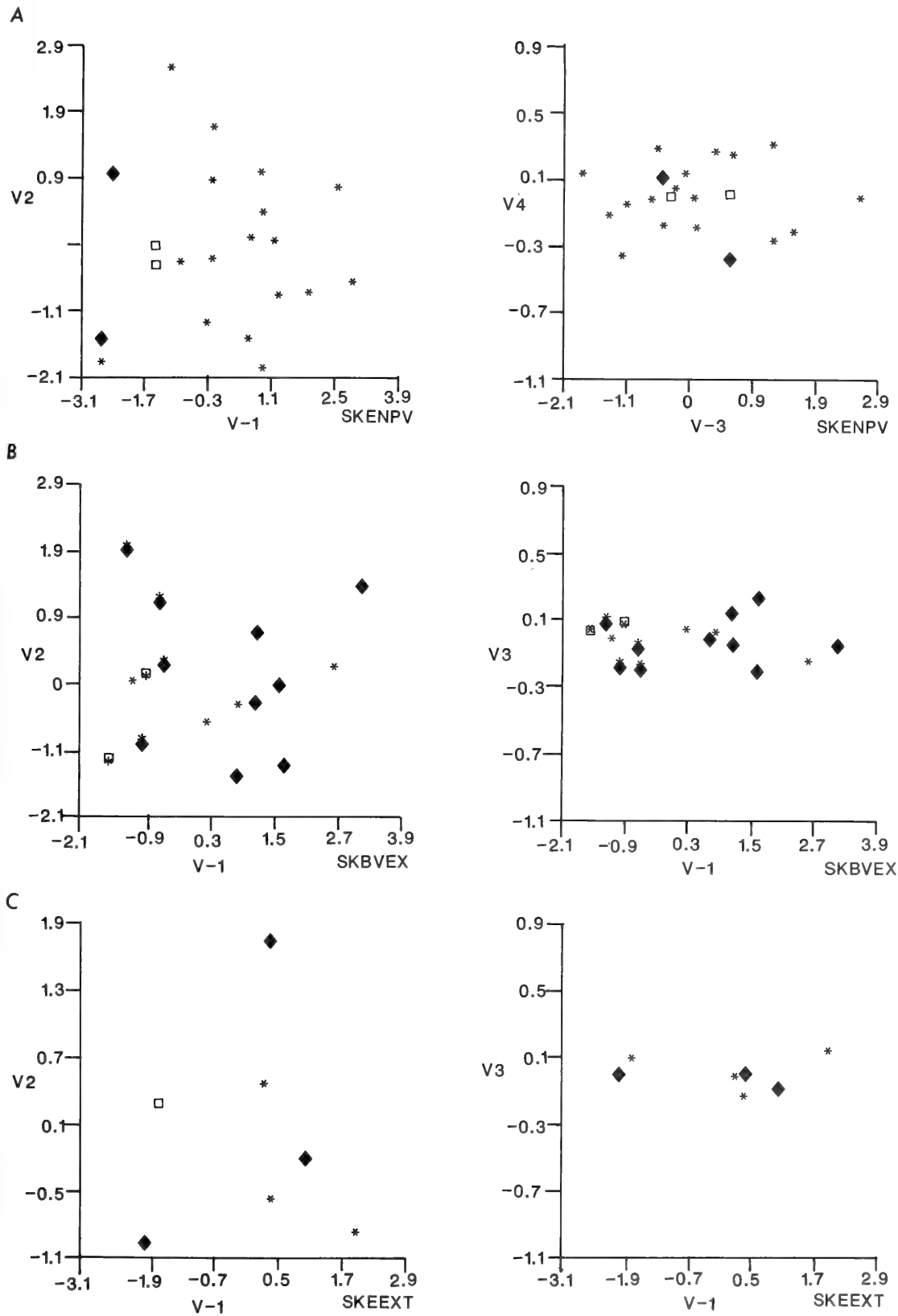
Fig. 18 Principal component analysis of *Skenidioides costatus*, from Kilbride (◆) and Kildare, Grange Hill House Cottage (˝) and Horizon 1 (□). A, pedicle valve internal moulds; B, brachial valve external moulds; C, pedicle valve external moulds.

Family **LINOPORELLIDAE** Schuchert & Cooper, 1931
Genus *SALOPIA* Williams, *in* Whittington & Williams 1955

Salopia sp.   Pl. 11, figs 18–20

MATERIAL AND LOCALITIES. Kildare, Grange Hill, Horizon 2: a single internal mould of a pedicle valve. Greenville-Moyne: 4 internal and 1 external moulds of brachial valves.

DESCRIPTION. *Ventral valve.* Interior, strongly convex mould, slightly sulcate, over half as deep as long, and slightly wider than long. Maximum width just anterior to hinge line, giving a subcircular outline to shell with high apsacline, but nearly catacline interarea. Short teeth are supported by divergent dental plates. Muscle field extends beyond dental-plates to about one-third of valve length. External ornament only seen where it is impressed around margins of shell interior.

Dorsal valve. Interior, gently convex in mould form, with low notothyrial platform between divergent brachiophores carrying a thin linear shaft which is continuous with a low median septum, extending to about mid-length. External ornament impressed slightly around margins of interior.

MEASUREMENTS (mm). BC 12758: X1 = 11·5, X2 = 12, X4 = 6, X9 = 4·5 (Pl. 11, fig. 19).

DISCUSSION. *Salopia* is known from the Llandeilo (Lockley & Williams 1981: 51) and Lower Caradoc (Williams 1963, 1974; Whittington & Williams 1955) of Wales and Shropshire. The single pedicle valve from Kildare is inadequate for formal comparison, but is apparently significantly deeper than described species. The sample from Greenville-Moyne is indistinctly preserved, and is lacking in pedicle valves, so cannot be directly compared to the Kildare specimen. The closest obvious comparison is with *Salopia salteri* (Davidson, 1869).

Family **SAUKRODICTYIDAE** Wright, 1964
Genus *SAUKRODICTYA* Wright, 1964

Saukrodictya cf. sp. A of Hints   Pl. 8, figs 8–15

cf. 1979   *Saukrodictya* sp. A, Hints: 57; pl. 2, fig. 10; pl. 4, figs 15–22.

MATERIAL AND LOCALITIES. Carrigadaggan: 1 internal and 3 external moulds of pedicle valves, 4 external moulds of indeterminate valves. Greenville-Moyne: 2 indeterminate external moulds.

DESCRIPTION. *Exterior.* Typical ornament of exopuncta, up to 6 radial rows, closely spaced, in the interspaces between narrow ribs. Interspaces are relatively wide and rounded. Ventral valve gently convex, wider than long.

Ventral interior. Nearly 50% wider than long. Gently convex profile, rectimarginate commissure. (Dorsal valve unknown).

DISCUSSION. The mould material, although very poor, is assigned to *Saukrodictya* rather than *Salacorthis* because of the typical pitted ornament found only in the interspaces and not on the thin ribs. The frequency of ribs is also greater than in *Salacorthis costellata* Williams (1974), the only known species, and the pedicle valves described here are not sulcate, as are those of *Salacorthis*.

There are a number of described species of *Saukrodictya*, but in all cases they are based on limited material and are not well known. The present material does not permit a detailed comparison with described species, but the illustrations of *Saukrodictya* sp. A by Hints (1979) from the Idavere and Johvi Stages in Estonia (L. Caradoc – *multidens* Biozone) are most similar to this material. The species apparently lacks the strong fold of *S. reticula* Vinassa, 1927 (Villas, 1985). It has a lower frequency of ribs than *S. rotundopora* Hints or *S. oblongatopora* Hints, both of which also have a fold. Similarly, *S. porosa* is sulcate and also has a greater rib frequency, though its general outline is similar (Havlíček 1977). The type species *S. hibernica* Wright (Wright 1964; see also Hiller, 1980) is strongly sulcate. However, Villas (1985) has suggested that *S. hibernica* may be conspecific with *S. reticula* (Vinassa, 1927), 'but there are too many gaps in the knowledge of 'British' and Sardinian *Saukrodictyae*'. The present sample unfortunately does nothing to clarify the definition of species, but is stratigraphically and biogeographically significant.

These are the oldest known occurrences of *Saukrodictya* in Ireland. *S. rotundopora* Hints (1979: 53) and *S. oblongatopora* Hints (1979: 55) are from approximately contemporaneous stages in the Middle Caradoc of Estonia. Other occurrences are Ashgill in age, including the type species *S. hibernica* from Portrane (Wright 1964: 216) and Wales (Hiller 1980: 165), *S. wrighti* from Belgium (Sheehan 1987) or from the Llandovery (*S.* sp. from Wales (*in* Temple, 1970: 32); *S.* sp. B from Estonia (Hints, 1979: 58)). According to Havlíček (1977) the oldest occurrence of species of *Saukrodictya* are *S. porosa* from the Liben and Letná Formations of Bohemia (Middle Llandeilo to Costonian) and in the Costonian/Harnagian of Portugal (Mitchell 1974). It would thus appear to have a Gondwanan origin and to have migrated northward, reaching Ireland by the Longvillian or earlier.

Superfamily **GONAMBONITOIDEA** Schuchert & Cooper, 1931
Family **KULLERVOIDEA** Öpik, 1934
Genus *KULLERVO* Öpik, 1934

Kullervo aff. *hibernica* Harper, 1952   Pl. 9, figs 1–10, 12–13

aff. 1952   *Kullervo hibernica* Harper: 100; pl. 6, figs 6–8.
aff. 1977   *Kullervo* aff. *hibernica* Harper; Brenchley *et al.*: 70.

PLATE 8

Figs 1–7 *Oanduporella* cf. *reticulata* Hints. Kildare, Grange Hill House Cottage. **1, 2**, BC 12709, external mould of brachial valve, and latex cast, × 10. **3, 4**, BC 12710a, internal mould of brachial valve, and latex cast, × 10. **5, 6**, BC 12710b, external mould of brachial valve, counterpart of Figs 3–4, latex cast, × 10. **7**, BC 12712, internal mould of brachial valve, × 72.

Figs 8–15 *Saukrodictya* cf. sp. A of Hints. Carrigadaggan. **8, 11**, BC 12713, external mould, latex cast and mould, × 10. **9, 10**, BC 12714, external mould and latex cast, × 10. **12**, BC 12715a, internal mould of pedicle valve, × 8. **13**, BC 12716b, latex cast of external mould, × 10. **14, 15**, BC 12715b, external mould of pedicle valve, counterpart of Fig. 12, latex cast and mould, × 10.

MATERIAL AND LOCALITIES. Carrigadaggan: 3 internal moulds and 5 external moulds of pedicle valves, 2 internal and 3 external moulds of brachial valves and 8 indeterminate external moulds. Kildare, Grange Hill, Horizon 1: 1 external mould of a pedicle valve and 2 fragments of internal moulds of pedicle valves. Greenville-Moyne: 3 internal and 3 external moulds of pedicle valves, 2 external moulds of brachial valves, and 2 indeterminate external moulds.

DESCRIPTION. *Exterior*. Strongly ventribiconvex *Kullervo* with pyramidal pedicle valve and maximum width along hinge line. Concave posterolateral flanks on extended hinge line, anterior slope evenly convex. Shallow median sulcus in brachial valve, but essentially rectimarginate commissure. Ventral interarea high, curved, apsacline near umbo, catacline near hinge. Dorsal interarea short, anacline. Ornament of distinctive reticulate pattern, of strongly developed concentric lamellae and regular radial ribs. Radial ornament absent on posterolateral flanks.

Ventral interior. Spondylium with hemisyrinx supported by well-developed median septum extending nearly to mid length. External ribs impressed on anterior margins of valve interior.

Dorsal interior. Cardinalia of thick divergent socket ridges about three times as long as wide, extending less than half valve width. Thin cardinal process in narrow space between their ends. Socket ridges merge anteromedially with thick notothyrial platform, itself passing into thick median ridge anteriorly. At about mid-length of valve the ridge tapers to a thin, low median septum, separating very poorly impressed adductor scars.

DISCUSSION. Harper's (1952) original description of *Kullervo hibernica* was based on limited material. In respect of the external ornament, overall shape and ventral interior the described material is comparable to the paratype material of *Kullervo hibernica* Harper from Grangegeeth (NMING: F14035, 14036). However, a single well-preserved brachial valve interior from Carrigadaggan (Pl. 9, figs 12, 13) shows some differences from the holotype of *hibernica* (NMING: F14034; Pl. 9, fig. 18), which is itself broken and missing posteriorly; in the *hibernica* holotype the impression of external ribs is more regular, stronger and abruptly and evenly terminated. In the Carrigadaggan specimen the ribs are variably impressed, also more irregular and longer. However, an additional broken, poor specimen does show a more regular and even impression of external ribs. In both specimens, a thick, well-developed median ridge, continuous with the notothyrial platform, tapers at about mid-length to a thin, low median septum between the anterior adductors. The most noticeable difference is in the anterior adductor scars. In *K. hibernica* they are very strongly impressed with

raised edges, but in the Carrigadaggan specimen they are barely seen and less divergent.

With such a small sample these differences are not deemed to justify erection of a new species. Larger samples are needed to clarify the relationship of the Irish specimens of *Kullervo* to each other and other poorly known species, especially since the material described herein is mostly fragmentary or broken. It is thus difficult to measure the important morphological characters, but the figured specimens show similar proportions to the type material. Other recent descriptions of *Kullervo* species, such as Whittington & Williams (1955) from the Derfel Limestone of Wales, Wright (1964) from the Portrane Limestone of eastern Ireland, and Hiller (1980) from North Wales, have all drawn attention to Öpik's original description of the genus (1934). In this, he defined four groups on the basis of external ornament. All the present material is similar to group 2, in particular *K. lacunata* Öpik, which has strong radial ribs in the middle sector but dominant concentric ornament on the ears. The material is unlike *K. complectens albida* which has a ventral sulcus bounded by stronger ribs. Consequently, although the type material is poorly known, this material is affiliated to *K. hibernica*. It is possible that larger collections of topotype material may show that *K. hibernica* is synonymous with the Kukruse (*N. gracilis*) form from Estonia, *K. lacunata*, or more likely that it is descended from that species, with an increase of radial ribs and stronger reticulation.

Superfamily **TRIPLESIOIDEA** Schuchert, 1913
Family **TRIPLESIIDAE** Schuchert, 1913
Genus *BICUSPINA* Havlíček, 1950

Bicuspina ?sp   Pl. 9, fig. 11

MATERIAL AND LOCALITY. Kilbride: 2 internal moulds of brachial valves, and one external mould fragment.

DISCUSSION. These two incomplete dorsal moulds could possibly be assigned to *Bicuspina*, or to the similar genus *Oxoplecia* which Carlisle (1979: 552) recorded from Kilbride. However, the overall shape, especially the very angular dorsal fold, suggests *Bicuspina* is more appropriate.

Superfamily **PLECTAMBONITOIDEA** Jones, 1928
Family **BIMURIDAE** Cooper, 1956
Genus *BIMURIA* Ulrich & Cooper, 1942

Bimuria cf. *dyfiensis* Lockley, 1980
Pl. 9, figs 14–17; Pl. 12, figs 1–9
?1977   *Bimuria* sp.; Mitchell: 95; pl. 19, figs 24–28.

PLATE 9

Figs 1–10, 12–13 *Kullervo* aff. *hibernica* Harper. Carrigadaggan. **1**, BC 12717, incomplete internal and external mould of pedicle valve, × 4. **2**, BC 12718a, internal mould of pedicle valve, × 2. **3, 7**, BC 12719, external mould of pedicle valve, and latex cast, × 2. **4, 5**, BC 12720, internal mould of pedicle valve, and latex cast, × 4. **6**, BC 12721, latex cast of external mould of pedicle(?) valve, × 4. **8**, BC 12718b, latex cast of external mould of pedicle valve, counterpart of Fig. 2, × 4. **9, 10**, BC 12722, external mould of brachial valve, latex cast and mould, × 4. **12, 13**, BC 12723, internal mould of brachial valve, latex cast and mould, × 4.

Fig. 11 *Bicuspina*? sp. Kilbride. BC 12724, internal mould of brachial valve, × 2.

Figs 14–17 *Bimuria* cf. *dyfiensis* Lockley. Ballykale. **14**, BC 12725, internal mould of pedicle valve, × 32. **15**, BC 12726, dorsal view of internal mould of pedicle valve showing strongly incurved umbo, × 32. **16**, BC 12727a, dorsal view of conjoined internal mould, × 32. **17**, BC 12728, internal mould of pedicle valve, × 32.

Fig. 18 NMING:F14034. Holotype of *Kullervo hibernica* Harper; an internal mould of a brachial valve from Grangegeeth, Co. Meath. × 4.

cf. 1980   *Bimuria dyfiensis* Lockley: 215, figs 60–62, 64–65.

MATERIAL AND LOCALITY. Ballykale: 16 internal moulds of pedicle valves, 3 internal moulds of brachial valves and 4 external moulds of pedicle valves.

DESCRIPTION. *Exterior.* Concavo-convex valves with pedicle valve umbo incurved and overlapping dorsal interarea. Rectimarginate, with subcircular outline. Both valves essentially smooth, with comae absent or very indistinct, resembling growth lines, in the brachial valve. Mean length about three-quarters of width.

Ventral interior. Simple teeth developed laterally for about one-third of the width of the valve but short anteromedially. A pinnate mantle canal pattern surrounding an undifferentiated muscle field is variably impressed (or preserved).

Dorsal interior. Low socket ridges nearly parallel to the hinge line. Prominent submedian septa and a thin median septum within a papillose bema.

MEASUREMENTS
Pedicle valve internal moulds:

Variates	X1	X2
Means	9·89	13·3
Sample size	16	16
Variance-covariance	12·21	11·36
Matrix		15·55

DISCUSSION. Specimens are too deformed for reliable quantitative study. The measurements taken are given above, but caution is advised in using them other than as a general guide to the species morphology, because of tectonic deformation. The Ballykale population of *Bimuria* is quite strongly deformed and flattened, so precise comparison with known Scoto-Irish species (*B.* cf. *buttsi* Cooper, *B. youngiana* Davidson, *B. youngiana recta* Williams) is not possible. Enough well-preserved specimens are described to justify assignment to *B.* cf. *dyfiensis*; the most significant feature of the species is the absence of comae. The size of the Ballykale sample is similar to the Welsh sample described by Lockley (1980) from the Gelli-grîn Formation of the Bala area of Wales. The lack of a fold and sulcus is distinctive in this population. *Bimuria* sp. from Kilbride (below) is of a much smaller mean size but otherwise shows very little difference from *B.* cf. *dyfiensis*. It is described under open nomenclature in the absence of dorsal interiors and exteriors, and because it is also similar in internal morphology and size to *B. youngiana recta* Williams. One poor pedicle valve exterior, however, shows no evidence of comae. The lack of comae is a feature of *Bimuria* sp. from the Ashgill Killey Bridge Formation at Pomeroy (Mitchell 1977), although that form is gently

sulcate. The size of specimens in this small sample is intermediate between *B.* cf. *dyfiensis* and *Bimuria* sp. from Kilbride. It seems likely that all three samples are closely related, but further specimens, preferably undeformed, are needed to verify this.

Bimuria sp.   Pl. 10, figs 1–7

MATERIAL AND LOCALITY. Kilbride: 21 internal moulds and one external mould of pedicle valves.

DESCRIPTION. *Exterior.* Unknown, except for one smooth, but poorly preserved valve.

Ventral interior. Strongly concavo-convex valve with strongly incurved umbo of pedicle valve overlapping dorsal interarea. Rectimarginate anterior commissure. Shell outline variable, from occasionally subcircular to sometimes transverse. Maximum width just anterior of hinge line, at about 27% of length. Length is always less than width; mean value is 78%. Depth of ventral valve is nearly half the length (44%).

Dorsal interior. Unknown.

MEASUREMENTS
Pedicle valve internal moulds (Kilbride):

Variates	X1	X2	X3	X4
Means	6·12	7·90	1·57	2·71
Sample size	19	20	20	20
Variance-covariance	2·62	2·51	0·89	1·16
Matrix		3·23	0·65	1·01
			0·69	0·44
				0·81

DISCUSSION. See *Bimuria* cf. *dyfiensis*, above.

Family **LEPTELLINIDAE** Ulrich & Cooper, 1936
Subfamily **LEPTELLININAE** Ulrich & Cooper, 1936
Genus and subgenus ***LEPTELLINA (LEPTELLINA)*** Ulrich & Cooper, 1936

Leptellina (Leptellina) cf. *llandeiloensis* (Davidson, 1883)   Pl. 10, figs 8–14

cf. 1883   *Leptaena llandeiloensis* Davidson: 171; pl. 12, fig. 26, *non* figs 27–29.
cf. 1917   *Plectambonites Llandeiloensis* (Davidson); Reed: 876; pl. 13, figs 32–34; pl. 14, figs 1–3.
cf. 1928   *Leptelloidea llandeiloensis* (Davidson); Jones: 477.
cf. 1962   *Leptellina llandeiloensis* (Davidson); Williams: 164; pl. 15, figs 27–29, 32.

PLATE 10

Figs 1–7 *Bimuria* sp. Kilbride. **1**, BC 12729, internal mould of pedicle valve, × 4. **2**, BC 12730, internal mould of pedicle valve, × 4. **3**, BC 12731, internal mould of pedicle valve, × 4. **4**, BC 12732, internal mould of pedicle valve, × 4. **5**, BC 12733, internal mould of pedicle valve, × 4. **6**, BC 12734a, internal mould of pedicle valve, × 4. **7**, BC 12734b, external mould of pedicle valve, counterpart of Fig. 6, × 4.

Figs 8–14 *Leptellina (Leptellina)* cf. *llandeiloensis* (Davidson). Carrigadaggan. **8, 9**, BC 12735, internal mould of pedicle valve, and latex cast, × 4. **10**, BC 12736, internal mould of pedicle valve, × 2. **11, 13, 14**, BC 12737, internal mould of pedicle valve, posterior view, latex cast, and dorsal view, × 2. **12**, BC 12738, latex cast of internal mould of brachial valve, × 4.

Figs 15–21 *Leptestiina oepiki* Whittington. **Figs 15–18**, Kildare, Grange Hill Horizon 1. **15**, BC 12739, internal mould of pedicle valve, × 4. **16, 17, 18**, BC 12740, internal mould of brachial valve, posterior and dorsal views of latex cast, and mould, × 4. **Figs 19–21**, Kilbride. **19**, BC 12741, internal mould of brachial valve, × 4. **20, 21**, BC 12742, internal mould of brachial valve, latex cast and mould, × 4.
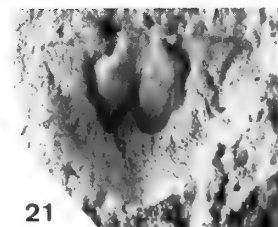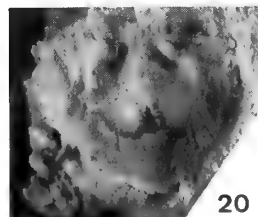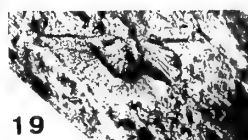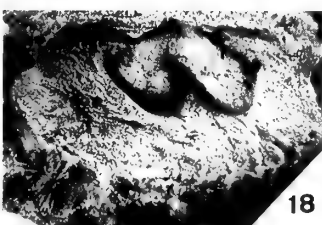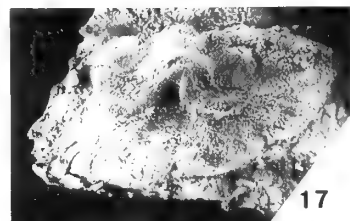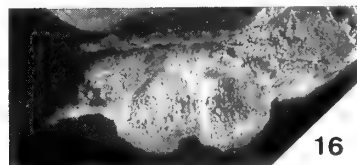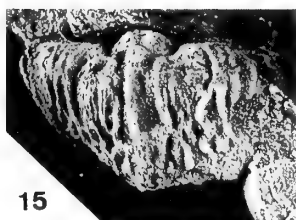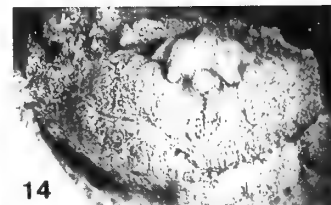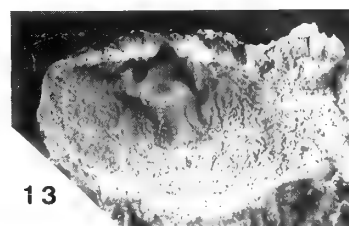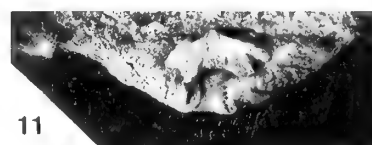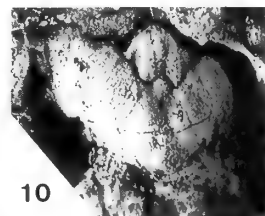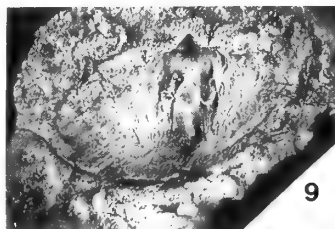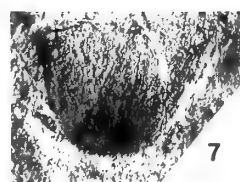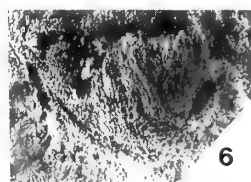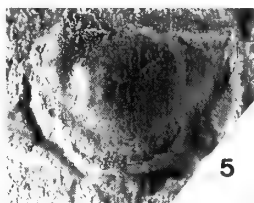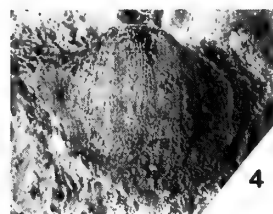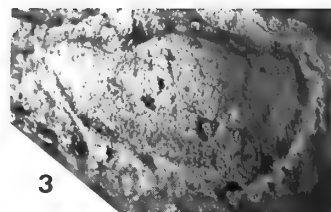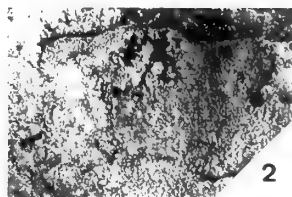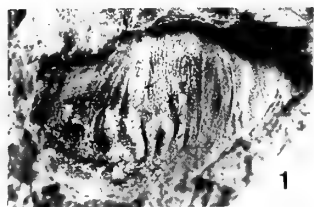
cf. 1977 *Leptellina* cf. *llandeiloensis* (Davidson); Mitchell: 72; pl. 13, figs 14–17.
cf. 1978 *Leptellina llandeiloensis* (Davidson); Cocks: 93.

MATERIAL AND LOCALITY. Carrigadaggan. 3 internal moulds of pedicle valves, and 3 incomplete internal moulds of brachial valves.

DESCRIPTION. *Exterior.* Unknown.

Ventral interior. Convex, transverse, nearly semicircular about 70% as long as wide and 40% as deep as long, rectimarginate anterior commissure. Maximum depth at about mid-length. Orthocline interarea about 20% of valve length. Deeply impressed large, quadrilobate muscle field 80% as long as wide, and extending anteriorly to about mid-length of valve. Small diamond-shaped platform anterior of and between the muscle field lobes, depressed in centre and with 4, 6 and 8 coarse pustules in a row on the anterior slope of the platform, sagittally. Delthyrium apparently open. Saccate pattern of mantle canals.

Dorsal interior. Large, well-defined platform is strongly elevated, ankylosed with a median septum and medially indented.

DISCUSSION. The present material is clearly inadequate for an unequivocal identification, in the absence of complete brachial valve interiors or any exteriors, but is assigned to *L.* cf. *llandeiloensis* because of the strong similarities to the material described by Mitchell (1977: 72) from the Caradoc Bardahessiagh Formation of Pomeroy. Previous descriptions have not recorded or remarked on the presence of a discrete median row of pustules anteriorly of the diamond shaped platform, but Mitchell's (1977: pl. 13, figs 14, 16) figured specimens clearly show them. What significance should be attached to this is unknown, since although Williams' (1962: pl. 15, fig. 28) specimens show them, he also figures a specimen of *Leptellina semilunata* (1962: pl. 15, fig. 23) which has a less ordered but equally strong row.

Family **LEPTESTIIDAE** Öpik, 1933, *emend.* Cocks & Rong, 1989
Genus *LEPTESTIINA* Havlíček, 1952

REMARKS. Cocks & Rong (1989: 116) reduced *Leptestiina* to a subgenus of *Leangella* Öpik, 1933. This is not followed here since, although Melou (1971) showed a phylogenetic sequence from *Leptestiina derfelensis* through *L. prantli* and *L. aonensis* to *Tufoleptina* (=*Leangella*), the early members of the lineage such as *Leptestiina oepiki*, *L. derfelensis* and *L. indentata* are sufficiently distinctive from *Leangella*, in the lack of a platform (*sensu* Cocks & Rong, 1989) anteriorly.

Leptestiina oepiki Whittington, 1938
Pl. 10, figs 15–21; Pl. 11, figs 1–6
1938 *Sampo oepiki* Whittington:255; pl. 10, figs 15–16; pl. 11, fig. 10.
1963 *Leptestiina oepiki* (Whittington); Williams: 428–430; pl.10, figs 15, 16, 19–21.
1978 *Leptestiina oepiki* (Whittington); Cocks: 94.
1989 *Leangella* (*Leptestiina*) *oepiki* (Whittington); Cocks & Rong: 116–117.

MATERIAL AND LOCALITIES. Kilbride: 6 internal and 1 external moulds of brachial valves; 4 internal and 1 external mould of pedicle valves. Kildare, Grange Hill, Horizon 1: 4 internal moulds of a pedicle valve and 2 internal moulds of brachial valves. Greenville-Moyne: 3 internal moulds of pedicle valves and 2 internal moulds of brachial valves.

DESCRIPTION. *Exterior.* Evenly concavo-convex valves, of semicircular outline. Pedicle valve about 60% as long as wide, and about 35% as deep as long. Ornamentation poorly-known, unequally parvicostellate with very fine costellae separated by few thicker ribs. Ventral interarea apsacline, dorsal interarea hypercline.

Ventral interior. Short blunt teeth supported by short receding dental plates, bordering a transversely subpentagonal muscle field which extends about 23% of valve length anteriorly. Length of muscle field about 50% of width. Deeply impressed vascula markings with lemniscate pallial sinus pattern.

Dorsal interior. Characteristically longitudinally and radially striated bema, bilobed and undercut with median incision and septum separating the two rounded lobes which originate laterally from the socket ridges, bounding oval sockets. Bema is about two-thirds as long as wide and extends anteriorly half the length of the valve.

DISCUSSION. The species *L. oepiki* is known from the Longvillian of Wales (Williams 1963: 428) and possibly the Actonian of Shropshire (Hurst 1979a: 275). Williams (1963: 430) noted the similarities between *L. oepiki* and the closely related Costonian species *L. derfelensis* Jones, 1928, from the Derfel Limestone in North Wales. He suggested the two may be synonymous, but the resolution of this must await further collections of *Leptestiina derfelensis* as well as more Irish material. The present sample is too small and poorly preserved to assess the variability of the species, particularly the external ornament. *L.* aff. *oepiki* is also known from Pomeroy, Co. Tyrone, in the Cautleyan Killey Bridge Formation (Mitchell 1977: 76); this also resembles *L. derfelensis* in some respects.

Harper (*in* Harper & Owen 1984: 29) revised the Upper Caradoc Norwegian species *L. indentata* (Spjeldnaes 1957:

PLATE 11
Figs 1–6 *Leptestiina oepiki* Whittington. Kilbride. **1**, BC 12743, internal mould of pedicle valve, × 4. **2, 3**, BC 12744, internal mould of brachial valve, and latex cast, × 4. **4**, BC 12745, internal mould of pedicle valve, × 4. **5**, BC 12746, internal mould of brachial valve, × 4. **6**, BC 12747, internal mould of brachial valve, × 4.
Figs 7–15, 17 *Leptestiina oepiki ampla* subsp. nov. Carrigadaggan. **7, 8**, **Holotype** BC 12748, internal mould of brachial valve, and latex cast, × 4. **9, 10**, BC 12749, internal mould of brachial valve, and latex cast, × 4. **11**, BC 12750, external mould of brachial valve, × 4. **12**, BC 12751, internal mould of pedicle valve, × 4. **13**, BC 12752, internal mould of pedicle valve, × 4. **14**, BC 12753, internal mould of pedicle valve, × 4. **15**, BC 12754, external mould of brachial valve, × 4. **17**, BC 12755, external mould of pedicle valve, × 4.
Fig. 16 *Reuschella*? sp. Kilbride. BC 12756, internal mould of pedicle valve, × 2.
Figs 18–20 *Salopia* sp. **Fig. 18**, Greenville-Moyne. BC 12757, internal mould of brachial valve, × 2. **19, 20**, Kildare, Grange Hill Horizon 2. BC 12758, internal mould of pedicle valve, and latex cast, × 2.
Figs 21–22 *Porambonites* sp. Kilbride. **21**, BC 12759, internal mould of pedicle valve, × 2. **22**, BC 12760, internal mould of pedicle valve, × 2.
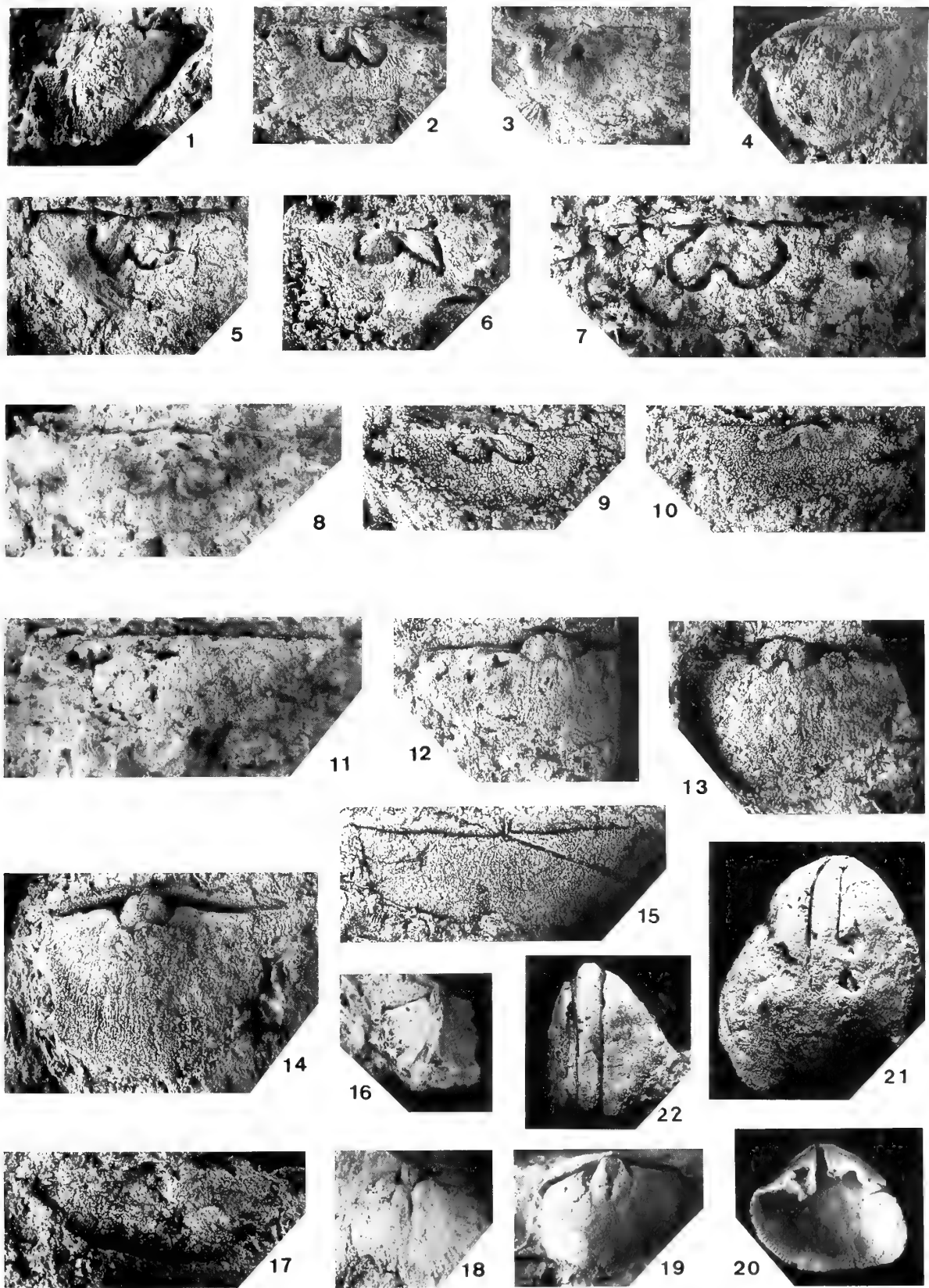
69). Although closely similar, this form has an apparently smooth bema and a greater frequency of accentuated ribs (at least 7) than *L. oepiki*. They synonymized a population from the Actonian of Shropshire which Hurst (1979*a*) had assigned to *L. oepiki*, based only on internal moulds. The one figured specimen of *L.* sp. (Hurst 1979*a*: 75, fig. 408), also from Shropshire and synonymized by Harper & Owen (1984), clearly shows a striated bema. Clearly, better preserved material of all these forms would be desirable, especially exteriors.

The inclusion of *L. indentata* in *Bilobia* by Cocks & Rong (1989: 114) is considered erroneous, since the species does not have the platform (*sensu* Cocks & Rong) near the anterior margin, a feature obviously present in *Bilobia* (Cocks & Rong 1989: 115, figs 70–71) but absent in *Leptestiina*. The bema is also more typically rounded and transverse, as in *Leptestiina* species, than the more complex divided bema of *Bilobia*.

Leptestiina oepiki ampla subsp. nov.   Pl. 11, figs 7–17

NAME. Latin; 'wide'.

DIAGNOSIS. Typical *Leptestiina oepiki* in all respects except for the significantly more transverse bema than in the nominate subspecies.

HOLOTYPE. BC 12748 (Pl. 11, figs 7, 8); paratypes BC 12749–55; Carrigadaggan.

MATERIAL AND LOCALITY. Carrigadaggan: 19 internal and 1 external moulds of pedicle valves; 2 internal and 2 external moulds of brachial valves.

DISCUSSION. The new subspecies accords with the material from Kilbride and Kildare, Grange Hill in all respects except for one feature. The bema is more transverse, the mean length being 46% of the width in two valves, as opposed to a mean of 70% for 6 valves from Kilbride and 63% for 2 valves from Grange Hill. It is difficult to assess the importance of this difference on such a small sample, but until the collection of more topotype material proves otherwise the Carrigadaggan population is assigned to the new subspecies *L. oepiki ampla*.

Family **XENAMBONITIDAE** Jones, 1928
Subfamily **AEGIROMENINAE** Havlíček, 1961
Genus *CHONETOIDEA* Jones, 1928

Chonetoidea abdita (Williams, *in* Whittington & Williams 1955)   Pl. 12, figs 10–16

1955 *Sericoidea abdita* Williams, *in* Whittington & Williams: 418; pl. 39, figs 83–85.

MATERIAL AND LOCALITY. Greenville: 21 external and 14 internal moulds of pedicle valves, 32 external and 12 internal moulds of brachial valves.

DESCRIPTION. *Exterior*. Concavo- or planoconvex, small shells of transversely semicircular outline, maximum width at hinge line. Cardinal angles acute to rectangular. Ventral valve most convex near umbo in lateral profile, about 15% as deep as long. Anterior profile rectimarginate, evenly convex, occasionally strongly convex medially. Length is 58% of the width (N = 53). Dorsal interarea hypercline and short, ventral interarea apsacline. Ornament quite variable, commonly finely costellate, occasionally parvicostellate, with about 10 ribs per mm, 2 mm anterior of the umbo.

Ventral interior. Very weakly impressed bilobed small muscle field. Small, simple teeth project dorsilaterally and are unsupported. Anterior margins of shell show feebly developed ribs, sometimes extending posteriorly to midvalve. Interspaces and valve interior characterized by minute pustules.

Dorsal interior. Short socket ridges ankylosed to small cardinal process. Thin median septum extends to mid-length of valve. Variable septule development, commonly 4, 5 or 6 septules arranged in an arc from the anterior end of the median septum. Occasionally second anterior arc of septules or very large circular pustules, third arc of coarse pustules rarely developed. External ornament impressed on finely pustulose interior.

Chonetoidea cf. *abdita* (Williams, *in* Whittington & Williams 1955)   Pl. 13, figs 1–4

MATERIAL AND LOCALITY. Kilbride: 6 internal and 2 external moulds of brachial valves, 14 internal and 7 external moulds of pedicle valves.

DESCRIPTION. *Exterior*. Small semicircular *Chonetoidea*, widest at the hinge line. Concavoconvex profile, with maximum convexity at umbo, about 20% as deep as long. Rectimarginate, with evenly convex anterior profile. Length about 64% of width. Hypercline, short dorsal interarea, apsacline ventral interarea. Variable ornament, parvicostellate to finely costellate, with occasional thickened ribs, with 15, 13 and 12 ribs per mm 2 mm anteriorly on 2, 1 and 1 valves.

Ventral interior. Small, weakly impressed muscle field. Unsupported, short simple teeth. Interior shows relatively strongly impressed ornament, particularly the accentuated ribs of parvicostellate specimens.

Dorsal interior. Thin median septum extends over half the valve length. Variable septule development in one or two arcs, commonly 4 to 7 septules in the posterior arc from the anterior end of the median septum. External ornament is impressed on interior, particularly the accentuated ribs of parvicostellate specimens.

DISCUSSION. The placing of *Sericoidea* in synonymy with

PLATE 12

Figs 1–9 *Bimuria* cf. *dyfiensis* Lockley. Ballykale. **1**, BC 12761, internal mould of pedicle valve, × 4. **2, 3**, BC 12762, internal mould of pedicle valve, and latex cast, × 48. **4, 5**, BC 12763, internal mould of brachial valve, and latex cast, × 48. **6**, BC 12764, dorsal view of conjoined internal mould, × 48. **7, 8**, BC 12765, external mould of brachial valve and part of pedicle valve, and latex cast showing interareas, × 48. **9**, BC 12766, external mould of brachial valve, × 48.

Figs 10–16 *Chonetoidea abdita* (Williams). Greenville. **10**, BC 12767, internal mould of brachial valve, × 10. **11**, BC 12768b, external mould of pedicle valve, × 10. **12**, BC 12769a, internal mould of brachial valve, × 4. **13**, BC 12770b, external mould of brachial valve, × 4. **14**, BC 12771, external mould of brachial valve, × 10. **15**, BC 12772a, internal moulds of adjoined pedicle and brachial valves, × 4. **16**, BC 12768a, internal mould of pedicle valve, counterpart of Fig. 11, × 10.
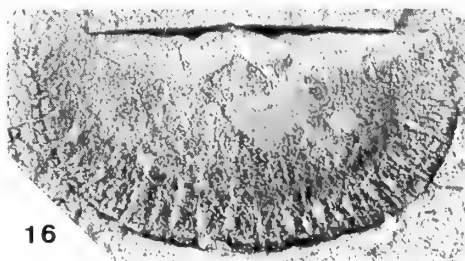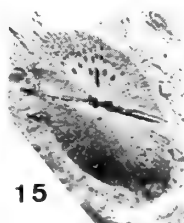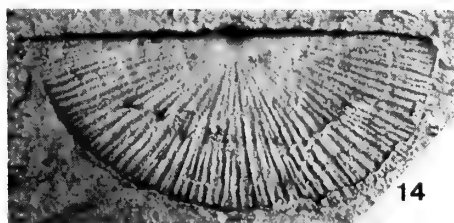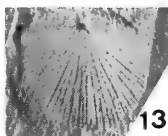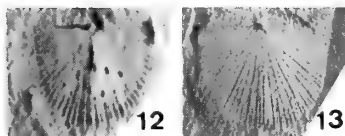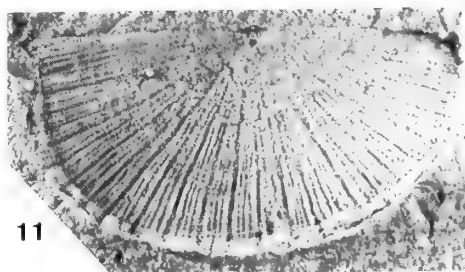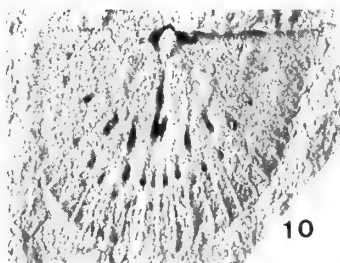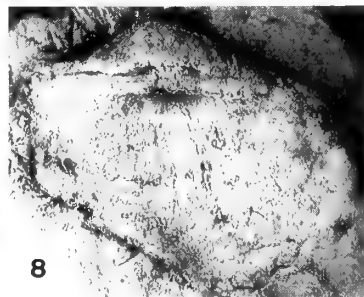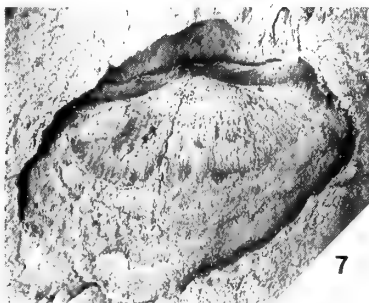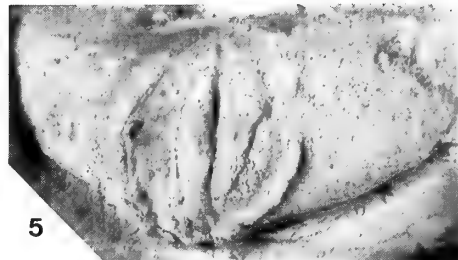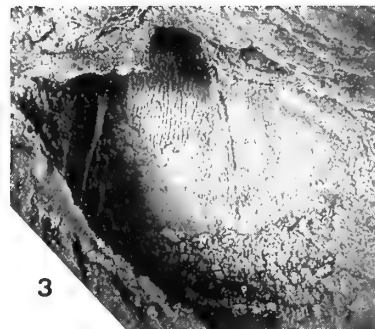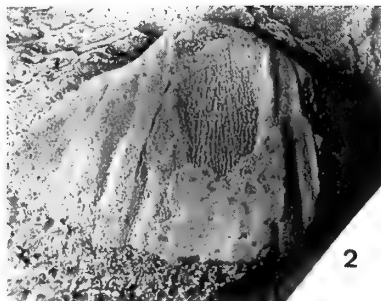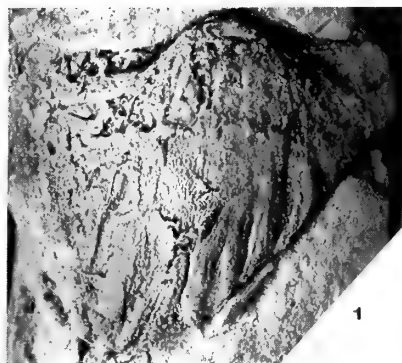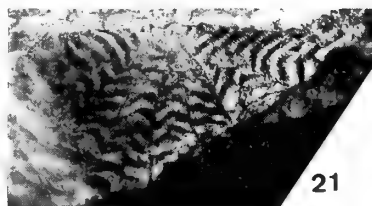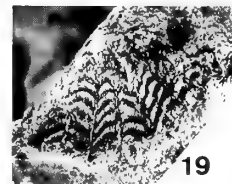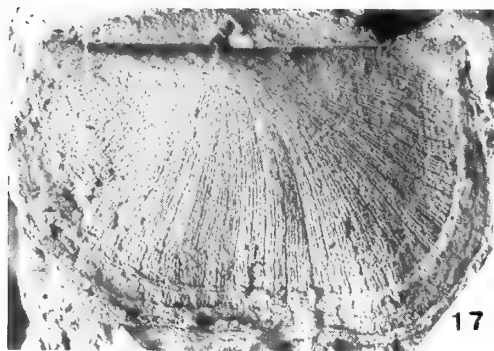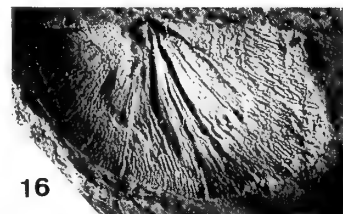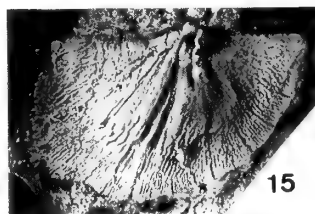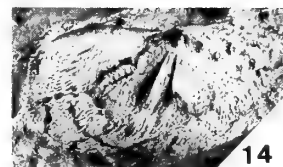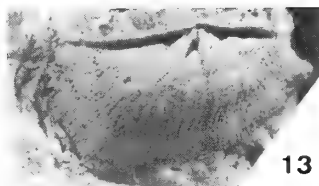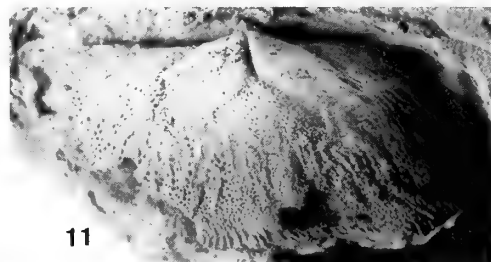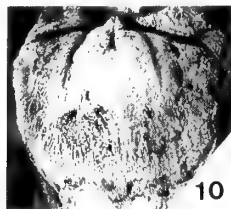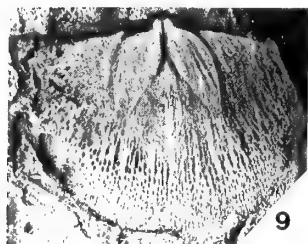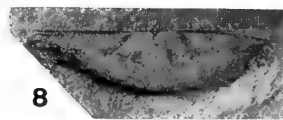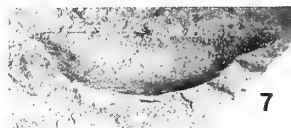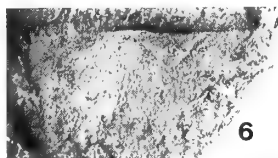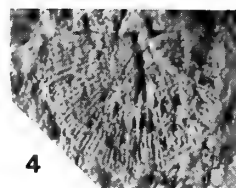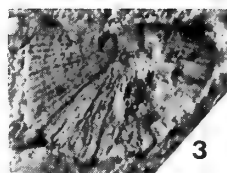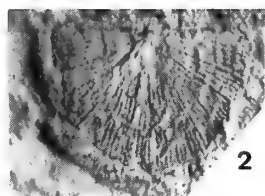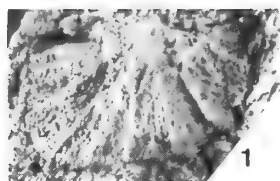
MEASUREMENTS
Brachial valve internal moulds (Greenville):

Variates	X1	X2	X24
Means	2·94	5·21	1·49
Sample size	12	12	9
Variance-covariance	0·50	0·0	0·24
Matrix		0·73	0·05
			0·16

Brachial valve external moulds (Greenville):

Variates	X1	X2
Means	2·87	5·17
Sample size	32	32
Variance-covariance	0·34	0·20
Matrix		1·22

Pedicle valve internal moulds (Greenville):

Variates	X1	X2	X4
Means	3·08	5·41	0·48
Sample size	14	14	9
Variance-covariance	0·28	0·05	−0·02
Matrix		1·15	−0·01
			0·01

Pedicle valve external moulds (Greenville):

Variates	X1	X2	X4
Means	2·99	5·29	0·52
Sample size	21	21	6
Variance-covariance	0·27	0·14	0·03
Matrix		1·06	0·03
			0·01

Chonetoidea by Cocks & Rong (1989) completes a task suggested by many authors, including Hurst (1979a: 281) and Young & Gibbons (1983), but not completed for lack of sufficient material. The two described species are a clear vindication of that decision, possessing characters variable between those previously characteristic of both genera. These include the external ornament (parvicostellate (*Sericoidea*) to finely costellate (*Chonetoidea*)) and septule arrangement

MEASUREMENTS
Brachial valve internal moulds (Kilbride):

Variates	X1	X2	X24
Means	2·00	3·25	1·05
Sample size	6	6	2
Variance-covariance	0·12	0·17	
Matrix		0·63	

Pedicle valve internal moulds (Kilbride):

Variates	X1	X2	X4
Means	2·19	3·39	0·44
Sample size	14	14	14
Variance-covariance	0·08	0·03	0·02
Matrix		0·29	0·01
			0·02

Pedicle valve external moulds (Kilbride):

Variates	X1	X2	X4
Means	2·17	3·49	0·54
Sample size	7	7	7
Variance-covariance	0·12	0·18	0·02
Matrix		0·55	0·05
			0·01

(few septules in one arc (*Sericoidea*) to many septules and more than one arc (*Chonetoidea*)). The interarea preservation is not good enough to discern whether canals are present, as defined by Mitchell (1977: 93) in *Chonetoidea*.

Although the generic assignment is clearly to *Chonetoidea*, the assignment of the two samples to *Chonetoidea abdita* and *Chonetoidea* cf. *abdita* is made with some hesitation. Other workers have found it difficult to distinguish species effectively on the basis of shape or outline. The only commonly variable characters found to be useful are the frequency of costellae and the arrangement and number of septules or sub-median septae in the lophophore platform of the brachial valve. Comparisons with described species are hindered by differences in numerical description. For example, older descriptions note the number of costellae per mm at the anterior margin irrespective of size, whilst later workers and my own counts were per mm at 2mm sagittally. Some recent work has reverted to marginal counts, e.g. Harper (1989). In

PLATE 13
Figs 1–4 *Chonetoidea* cf. *abdita* (Williams). Kilbride. **1**, BC 12773, internal mould of pedicle valve, × 10. **2**, BC 12774b, external mould of brachial valve, × 10. **3**, BC 12808, external mould of pedicle valve, × 10. **4**, BC 12774a, internal mould of brachial valve, counterpart of Fig. 2, × 10.
Figs 5–8 *Anisopleurella* cf. *multiseptata* (Williams). Greenville-Moyne. **5**, BC 12776a, internal mould of brachial valve, × 4. **6**, BC 12776b, external mould of brachial valve, counterpart of Fig. 5, × 4. **7**, BC 12777b, external mould of pedicle valve, × 2. **8**, BC 12777a, internal mould of pedicle valve, counterpart of Fig. 7, × 2.
Figs 9–18 *Sowerbyella sericea* (J. de C. Sowerby). Figs 9–14,17, Kildare, Grange Hill Horizon 1. **9**, BC 12778, internal mould of pedicle valve, × 4. **10**, BC 12779, internal mould of pedicle valve, × 4. **11**, BC 12780, internal mould of pedicle valve, × 4. **12**, BC 12781, internal mould of pedicle valve, × 4. **13**, BC 12782, internal mould of pedicle valve, × 4. **14**, BC 12783, internal mould of brachial valve, × 4. **17**, BC 12785, external mould of brachial valve and interareas, × 4. **Figs 15, 16, 18**, Kilbride. **15, 16**, BC 12784, internal mould of brachial valve, latex cast and mould, × 4. **18**, BC 12786, external mould of brachial valve, × 4.
Figs 19–22 *Ptychoglyptus* sp. Kilbride. All incomplete external (?) moulds. **19**, BC 12787, × 4. **20**, BC 12788, × 4. **21**, BC 12789, × 5. **22**, BC 12790, × 4.

addition, the precision of the counts is slightly suspect, given the very small size of specimens.

Notwithstanding the problem of definition of septules *versus* coarse pustules (see Lockley, 1980: 215), the development of second arcs and more septules is not dependent on size, since smaller specimens can have as many or more than medium or large specimens in the two samples. Although Lockley (1980: 214, fig. 63) gives a useful table of the number of septules in different size classes, it is not clear whether this is total numbers or of one particular arc where more than one is developed. In the Greenville sample, 4 out of 12 measured brachial valves have second arcs developed with 2, 9, 12 and 13 septules present, and the third one has a third arc developed with 11. In isolation, these would probably be identified as *Chonetoidea papillosa* or *Chonetoidea radiatula*. In the Kilbride species, 2 out of 6 had a second arc with 6 and 12 septules.

Neither species is like the type species *Chonetoidea restricta* (Hadding) or *Chonetoidea homolensis* Havlíček (see Harper, 1989) as the median septum and septule arcs in these species are contained within the posterior half of the shell. Although contemporaneous, *Chonetoidea* sp. from the Gelli-grîn Formation (Williams 1963) differs in having a platform developed by coalescence of strong septules. Percival (1979: 115) described two species, *Chonetoidea sejuncta* and *Chonetoidea minor*, which together with *Chonetoidea virginica* (Cooper, 1956) form a distinct species group. These have a thin median septum extending up to mid-length, but the 2 to 4 pairs of discrete small septules are positioned laterally in a row, not arcuate as in the Greenville and Kilbride samples.

In summary, both the Leinster species are best assigned to the *Chonetoidea abdita* Williams form, as emended by Lockley (1980). The original species description was limited owing to paucity of material. Williams has compared Lower Caradoc material from the Balclatchie Group (1962) of Girvan and the Soudleyan Hagley Shales of Shropshire (1974) with the Welsh form, and noted little difference. Although the poorly preserved Kilbride form is here described separately, as it is somewhat deeper and has a slightly greater frequency of costellae than the Greenville sample, these differences are probably not important. All the forms compared to the species, including these samples, are probably displaying a range of variation wider than that normally seen in the often small samples available. The actual data for septule and costellae numbers are given for comparison (Tables 21–22).

Table 21 Frequency of counts of costellae per mm at 2 mm sagitally for *Chonetoidea abdita* from Greenville, *Chonetoidea* cf. *abdita* from Kilbride, *Chonetoidea* cf. *abdita* from Shelva (data from Williams, 1974) and at the anterolateral margins for *Chonetoidea* aff. *abdita* from Girvan (data from Williams, 1962).

8	9	10	11	12	13	14	15	16	Total	
4	8	12	10	3	3	2	3	1	46	*C. abdita* Greenville
			1	1		2			4	*C.* cf. *abdita* Kilbride
		3	3	1					7	*C.* cf. *abdita* Shelve
		3	7	8	6	3	1		28	*C.* aff. *abdita* Girvan

Table 22 Distribution of various types of lophophore platform, with number of septules on either side of median septum (MS) in columns for *Chonetoidea abdita* samples. Data for *Chonetoidea abdita* from Greenville (left columns) and *Chonetoidea* cf. *abdita* from Kilbride (central columns) based on posterior arc of larger septules when more than one developed. Date for *Chonetoidea* aff. *abdita* from Girvan (right columns) modified from Lockley (1980).

Length (mm)	MS	1	2	3	Total
0·6–1·0	0 0 3				0 0 3
1·1–1·5	0 0 1	0 0 1		0 1 0	0 1 2
1·6–2·0		0 0 2	0 2 0	1 0 4	1 2 6
2·1–2·5		0 0 2	2 1 0	1 1 3	3 2 5
2·6–3·0			3 0 0	0 0 4	3 0 4
3·1–3·5			1 0 0	2 0 3	3 0 3
3·6–4·0				2 0 0	2 0 0
	0 0 4	0 0 5	6 3 0	6 2 14	12 5 23

Genus **ANISOPLEURELLA** Cooper, 1956

Anisopleurella cf. **multiseptata** (Williams, *in* Whittington & Williams 1955)   Pl. 13, figs 5–8

MATERIAL AND LOCALITY. Greenville-Moyne: 8 internal and 2 external moulds of pedicle valves, 2 internal and 5 external moulds of brachial valves.

DISCUSSION. The sparse material, especially brachial valve interiors, is inadequately preserved and moderately deformed, making a specific determination difficult. Brenchley *et al.* (1977) recorded *Anisopleurella* aff. *multiseptata* Williams from this locality, but although similar to that species, the sample is apparently more transverse. Lockley (1980), however, compared a single pedicle valve from the Gelli-grîn Formation of Bala to the species *A. multiseptata* which appears similar to the material from Greenville-Moyne. The exteriors are poor but show the essentially smooth exterior ornamented by a few widely-spaced primary costae, and Brenchley *et al.* (1977) are followed in comparison of this species to *A. multiseptata* Williams.

Family **SOWERBYELLIDAE** Öpik, 1930
Subfamily **SOWERBYELLINAE** Öpik, 1930
Genus and subgenus **SOWERBYELLA (SOWERBYELLA)** Jones, 1928

Sowerbyella sericea (J. de C. Sowerby, 1839)
Pl. 13, figs 9–18

1839   *Leptaena sericea* J. de C. Sowerby, *in* Murchison: 636; pl. 19, fig. 1.
1928   *Sowerbyella sericea* (J. de C. Sowerby) Jones: 414; pl. 21, figs 1–4.
1963   *Sowerbyella sericea* (J. de C. Sowerby); Williams: 430–432; pl. 11, figs 1–9.
1970   *Sowerbyella sericea* (J. de C. Sowerby); Bretsky: 85–87; pl. 12, figs 3–6; pl. 13, figs 1–4.
cf.1974 *Sowerbyella sericea* (J. de C. Sowerby); Williams: 134–135; pl. 24, figs 11–14, 16.
1978   *Sowerbyella sericea* (J. de C. Sowerby); Cocks: 98.

1979a *Sowerbyella sericea* (J. de C. Sowerby); Hurst: 278; figs 412–432.

MATERIAL AND LOCALITIES. Kildare, Grange Hill, Horizon 1: 3 external and 15 internal moulds of pedicle valves; 7 external and 4 internal moulds of brachial valves. Kildare, Grange Hill, Horizon 2: 2 internal moulds of pedicle valves. Kilbride: 9 external and 17 internal moulds of pedicle valves, 7 external and 2 internal moulds of brachial valves. Carrigadaggan: 1 internal mould of a pedicle valve; 4 external and 2 internal moulds of brachial valves.

DESCRIPTION. *Exterior.* Semicircular outline, cardinal angles acute in smaller specimens, becoming rectangular in older stages. Concavo-convex shells, with median fold occasionally developed in pedicle valve, and concave flanks on pedicle valve. Length about 55–60% of the width, and depth about one third of the length in the pedicle valve. Radial ornamentation unequally parvicostellate, but quite variable, with 6–10 costellae per mm, 5 mm anteromedially of the umbo, segregated into sectors about 1 mm wide if not finely costellate. Occasionally a few pairs of rugae developed in posterolateral areas. Dorsal interarea very short, flat and cataline, ventral interarea curved and apsacline.

Ventral interior. Bilobed, divergent diductor muscle scars about 0·7 as long as wide, extending anteriorly for about one-third of valve length. Adductor scars separated posteriorly by thin median septum extending for 15–20% of valve length before bifurcating. Diductors widely separated anteriorly and split by divergent vascula media bounded by lateral ridges. Lemniscate pallial sinus pattern, with papillose anterior surface. Small teeth with obsolescent dental plates in adults.

Dorsal interior. Undercut cardinal process fused with widely divergent socket ridges. The bases of the socket ridges are continuous with two low ridges that rise in height anteriorly to become prominent sub-median septa extending about two-thirds of valve length. Sub-median septa diverge slightly, so that anterior separation is about one-third of their length. Low, small median septum and thinner, low, radial ridges across bema occasionally developed. Lemniscate pallial sinus pattern, and papillose interior anterior of the bema.

DISCUSSION. Although differing slightly in some proportions, from each other and from the type material, the differences are not significant, given the variability known in stocks of *Sowerbyella* (Cocks & Rong 1989: 139) and do not justify erection of a subspecies. A few of the measured specimens are also slightly distorted so the reliability of the statistics is low, but is presented as a general assessment of the morphology. Material from the Grange Hill, Carrigadaggan and Kilbride populations is all referred to the type species *S. sericea* (J. de C. Sowerby). The type species was revised by Williams (1963), and Hurst (1979a) figured a large sample of this species from the Woolstonian of south Shropshire to illustrate the variability within the species. The number of dorsal valves is small, but plots of the first four eigenvectors (Fig. 19) from a principal component analysis of pedicle valves from Kildare, Grange Hill and Kilbride shows no differences between the samples, except for overall size where vector 1 shows some differentiation. The Kilbride population has a smaller mean size.

MEASUREMENTS
Brachial valve external moulds (Kilbride):

Variates	X1	X2	X4
Means	6·83	1·21	1·35
Sample size	7	7	6
Variance-covariance	2·08	4·46	0·27
Matrix		12·51	0·57
			0·26

Pedicle valve internal moulds (Kilbride):

Variates	X1	X2	X4	X9	X10	X24
Means	5·51	9·42	1·83	1·43	2·10	0·77
Sample size	17	17	16	6	6	9
Variance-covariance	4·06	4·79	1·11	1·08	1·74	0·78
Matrix		0·70	0·23	0·43	0·28
			0·23	0·27	0·19
				0·49	0·24
					0·15

Brachial valve internal moulds (Kildare, Horizon 1):

Variates	X1	X2	X3	X22	X23
Means	9·38	1·78	2·85	6·08	1·95
Sample size	4	4	4	4	4
Variance	1·17	6·09	0·37	0·32	0·01

Brachial valve external moulds (Kildare, Horizon 1):

Variates	X1	X2	X4
Means	7·96	1·43	1·38
Sample size	7	7	6
Variance-covariance	13·43	17·64	1·55
Matrix		32·97	3·44
			0·57

Pedicle valve internal moulds (Kildare, Horizon 1):

Variates	X1	X2	X4	X9	X10	X24
Means	9·47	15·2	3·53	4·06	5·76	2·20
Sample size	15	15	15	14	14	14
Variance-covariance	3·61	4·97	0·69	1·88	2·33	0·86
Matrix		16·24	2·79	2·62	5·77	1·54
			1·48	0·52	1·27	0·29
				1·24	1·38	0·51
					2·62	0·77
						0·43

Pedicle valve external moulds (Kildare, Horizon 1):

Variatesa	X1	X2	X4
Means	9·47	16·0	3·27
Sample size	3	3	3
Variance	1·04	2·82	0·22

Subfamily **PTYCHOGLYPTINAE** Cooper, 1956
Genus *PTYCHOGLYPTUS* Willard, 1928

Ptychoglyptus sp.   Pl. 13, figs 19–22

MATERIAL AND LOCALITY. Kilbride: All material incomplete; one internal and one external moulds of a pedicle valve, one internal and one external moulds of a brachial valve, and 8 indeterminate moulds.

DESCRIPTION. Characteristic *Ptychoglyptus* rugae with a wavelength of 2 per mm, separated into discontinuous arcuate chevron-like pattern by strong radial costellae. Whole of surface, including rugae, sculpted with fine radial lines. Straight hinge line and slight rafinesquinoid convexity in pedicle valve. The dorsal interior is inadequately known.

MEASUREMENT. One specimen shows most of half a hinge line and gives a minimum hinge width of 21 mm.

DISCUSSION. The material is too fragmentary to justify a specific determination. It appears to be unlike *P. ? kindlei* Cooper (1956) which has a geniculate anterior, and also unlike *P. ? matura* Cooper (1956) which is non-rugose in the anterior half. It is comparable to *P. virginiensis* Willard (1928) in most respects except for the rugose sculpture. As Williams (1962) noted, this species has rounded crests to the rugae and is generally symmetrical or asymmetrical with steeper posterior slopes. Williams (1962) described three specimens of *P.* cf. *valdari* from Balclatchie, near Girvan in Scotland, with sharply asymmetrical rugae, and three with rugae overfolded in an anterior direction. The material from Kilbride most closely resembles this species since the crests are sharp and asymmetrical. The posterior slope is steeper but in some rugae there is an anteriorly deflected crest, creating an overfolded appearance, but it is variably developed within single specimens.

Superfamily **STROPHOMENOIDEA** King, 1846
Family **STROPHOMENIDAE** King, 1846
Subfamily **STROPHOMENINAE** King, 1846
Genus *STROPHOMENA* Rafinesque, 1825

Strophomena ? sp   Pl. 14, figs 13, 6

MATERIAL AND LOCALITY. Kildare, Grange Hill, Horizon 1: 2 external and 1 internal moulds of a pedicle valve.

DESCRIPTION. Gently, evenly convex pedicle valve with very shallow sulcus. Interarea high, apsacline about 14% as long as the valve. Simple triangular teeth supported by short divergent dental plates. Delthyrium almost completely closed by convex pseudodeltidium. Faint transverse grooves and ridges on the interarea near the hinge line. Interior shows

impression of ornament throughout, especially at margins. External ornament finely costellate with about 6 ribs per mm at 5 mm growth stage. Strong concentric, accentuated growth lines on exterior of shell.

MEASUREMENTS. BC 12791a & b: X1 = 28 mm, X2 = 21 mm, X4 = 3 mm, X6 = 38 mm; X1/X2 = 0·75, X4/X1 = 0·11, X6/X1 = 0·14 (Pl. 14, figs 1–3, 6).

DISCUSSION. Although the unequally parvicostellate ornament is lacking, the single valve part and counterpart moulds are questionably assigned to *Strophomena*, as the general morphology corresponds to the genus in other aspects. However it is 75% as wide as long, unlike species from Wales that are wider than long; there is no apparent deformation of the specimen.

Genus *KJERULFINA* Bancroft, 1929

Kjerulfina ? sp.   Pl. 14, fig. 7

MATERIAL AND LOCALITY. Kildare, Grange Hill, Horizon 1: a single internal mould of pedicle valve, incomplete.

MEASUREMENTS. BC 12792: X1 = 15 mm, X4 = 33 mm (Pl. 14, fig. 7).

DISCUSSION. This incomplete mould has an initially gently convex profile, but deflects abruptly in a ventral direction before geniculating sharply in a dorsal direction. It is moderately wrinkled by rugae posterolaterally and is finely ornamented by costellae impressions. The dental plates are divergent, short and curving. The specimen exhibits similarities to *Kjerulfina*, one species of which, *K. broeggeri*, has similar sporadic dorsally directed geniculation. Further material is required to reach a better identification.

Subfamily **RAFINESQUININAE** Schuchert 1893
Genus *RAFINESQUINA* Hall & Clarke 1892

Rafinesquina sp.   Pl. 14, figs 4–5, 8–10, 14–17

MATERIAL AND LOCALITY. Kildare, Grange Hill House Cottage: 5 internal and 5 external moulds of pedicle valves, 8 internal and 4 external moulds of brachial valves, 4 indeterminate external moulds and 3 indeterminate internal moulds, mostly fragmentary.

DISCUSSION. The best specimens of this genus are figured to show the typical form of the sample, but it is not described pending collection of more material to assess the morphological variation. It shows typical concavo-convex form, and unequally parvicostellate ornamentation. However, there are few modern descriptions of the genus from Britain or Ireland

PLATE 14

Figs 1–3, 6 *Strophomena*? sp. Single specimen from Kildare, Grange Hill Horizon 1. **1, 2**, BC 12791b, external mould of pedicle valve, and latex cast, × 2. **3, 6**, BC 12791a, counterpart internal mould of pedicle valve, and latex cast, × 2.

Fig. 7 *Kjerulfina*? sp. Kildare, Grange Hill Horizon 1. BC 12792, internal mould of pedicle valve, × 2.

Figs 4–5, 8–10, 14–17 *Rafinesquina* sp. Kildare, Grange Hill House Cottage. **4, 5**, BC 12793, internal mould of brachial valve, latex cast and mould, × 2. **8**, BC 12794, internal mould of pedicle valve, × 175. **9**, BC 12795b, external mould of pedicle valve, × 2. **10, 14**, BC 12795a, internal mould of pedicle valve, counterpart of Fig. 9, latex cast and mould, × 2. **15**, BC 12796b, external mould of brachial valve, × 2. **16, 17**, BC 12796a, internal mould of brachial valve, counterpart of Fig. 15, latex cast and mould, × 2.

Figs 11–13 *Hedstroemina* sp. Kildare, Grange Hill Horizon 1. **11**, BC 12797a, internal mould of pedicle valve, × 2. **12**, BC 12798, internal mould of pedicle valve, × 2. **13**, BC 12799, internal mould of pedicle valve, × 2.
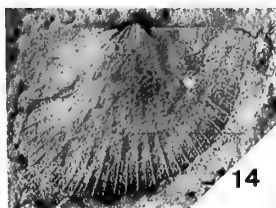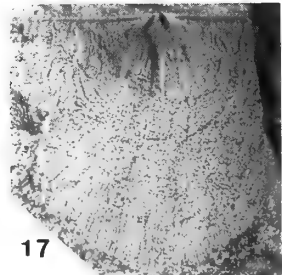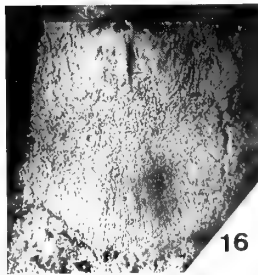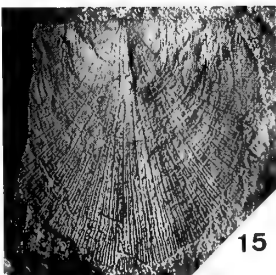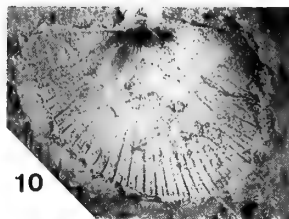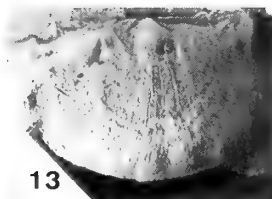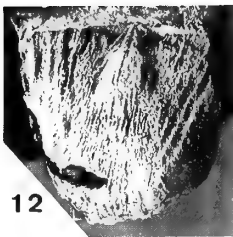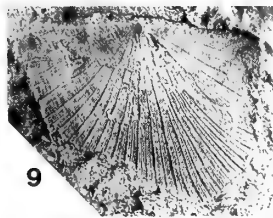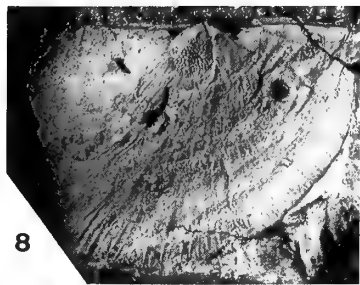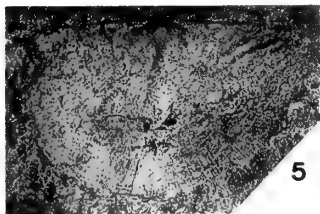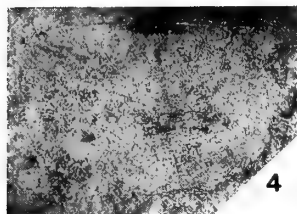
and few well-defined species. Lamont (1953) claimed the record by Reynolds & Gardiner (1896) of *Strophomena expansa* J. de C. Sowerby should be *Rafinesquina concentrica* (Portlock) var. However, specimens collected by Lamont (NMING: F18662, F18663, F18599, F18611) from this locality are labelled as '*R. eirenach* Lamont'. No publication of this species name is known, and the material is kept in open nomenclature, pending further collection and analysis.

Family **STROPHOMENIDAE** King, 1846
Genus ***HEDSTROEMINA*** Bancroft, 1929

Hedstroemina sp.   Pl. 14, figs 11–13

MATERIAL AND LOCALITIES. Kildare, Grange Hill, Horizon 1: 3 internal and 3 external moulds of pedicle valves; 3 external moulds of brachial valves. Kildare, Grange Hill, Horizon 2: 7 internal moulds of pedicle valves.

DISCUSSION. The restricted sample makes identification problematical, given the wide variation within the genus and the closely related *Kjaerina*. As also noted by Williams (1963: 460), in a very small Bala sample the lack of a strong median rib invites allocation to *Hedstroemina* rather than *Kjaerina*. Hurst (1979a: 288) notes four characteristics in Upper Caradoc populations which could consistently be used to separate them, one being the development of weak rugae which is also seen in this material.

Family **LEPTAENIDAE** Cooper, 1956
Genus ***LEPTAENA*** Dalman, 1828

Leptaena sp.   Pl. 15, figs 1–7

MATERIAL AND LOCALITIES. Kildare, Grange Hill, Horizon 1: 6 internal and 3 external moulds of pedicle valves; 5 external moulds of brachial valves; 6 indeterminate exterior fragments and 1 conjoined internal mould. Kildare, Grange Hill, Horizon 2: 1 internal and 1 external moulds of pedicle valves; 1 internal and 2 external moulds of brachial valves, all incomplete.

DISCUSSION. The small fragmentary sample is insufficient for statistical comparison with other known *Leptaena* species, and is left under open nomenclature pending better material to assess the variability. Inspection of the ventral muscle field, however, suggests it may be conspecific with *L. ventricosa* Williams from the Longvillian Gelli-grîn Group of Bala.

Fig. 19 Principal component analysis of *Sowerbyella sericea* (pedicle valve internal moulds) from Kildare, Grange Hill Horizon 1 (▼), Kilbride (*) and Carrigadaggan (□). A, Plot of vector 1 against vector 2; B, Plot of vector 3 against vector 4; C, Plot of vector 2 against vector 3.
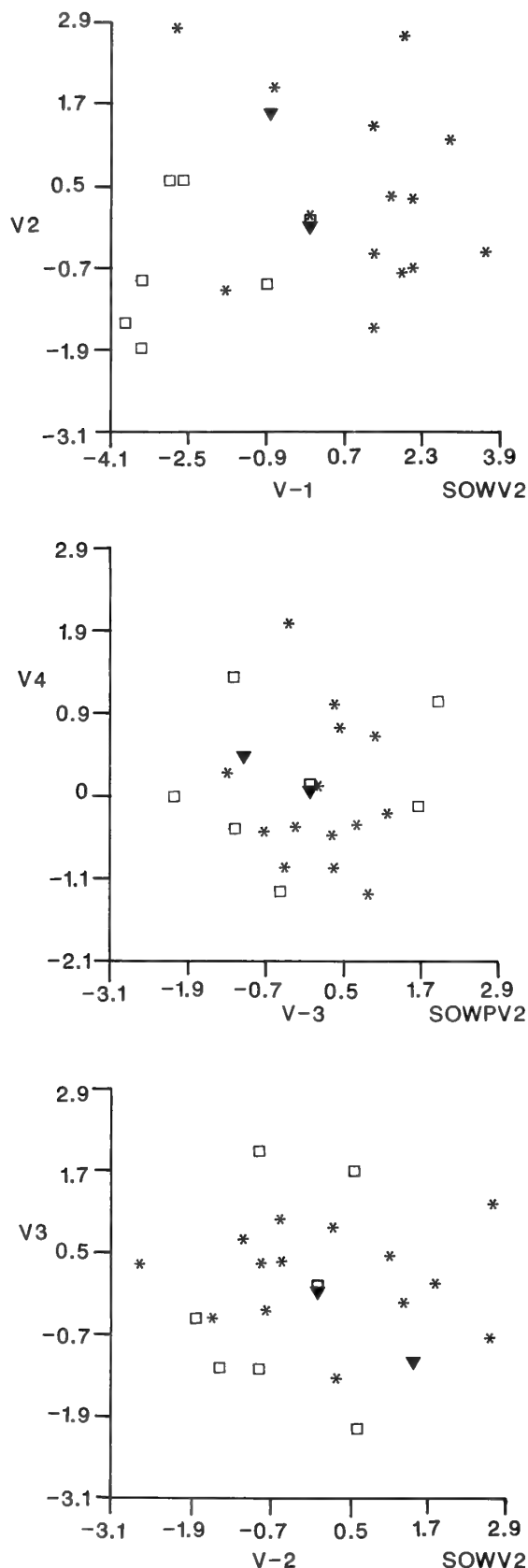
Family **STROPHEODONTIDAE** Caster, 1939
Subfamily **STROPHEODONTINAE** Caster, 1939
Genus *HIBERNODONTA* Harper & Mitchell, *in* Harper *et al.* 1985

Hibernodonta ? sp.   Pl. 15, figs 8–10

MATERIAL AND LOCALITY. Kildare, Grange Hill House Cottage: 3 internal and 1 external mould of brachial valves, 2 external moulds of pedicle valves and 3 indeterminate external moulds.

DISCUSSION. The genus and species *H. praeco* were first described from the Clashford House Formation at Herbertstown, Co. Meath by Harper & Mitchell (*in* Harper *et al.* 1985). As an early stropheodontid, the small rafinesquinid-like valves have denticulate hinge lines. The specimens here are tentatively assigned to *Hibernodonta*, since there is an appearance of denticulation on the hinge line, as well as definite denticulate teeth. However, the material is poorly preserved and only three valves have the hinge area present, although the size of the sample is larger than that of the type species. There is no thickened median rib. Until better preserved specimens are collected the material can only be questionably assigned to *Hibernodonta*; it may equally be a strophomenoid species which developed denticulate teeth and sockets, other cases of which are discussed by Harper *et al.* (1985).

Superfamily **PORAMBONITOIDEA** Davidson, 1853
Family **PORAMBONITIDAE** Davidson, 1853
Genus *PORAMBONITES* Pander, 1830

Porambonites sp.   Pl. 11, figs 21–22

MATERIAL AND LOCALITY. Kilbride: 2 internal moulds of pedicle valves.

DESCRIPTION. *Ventral interior*. Large valves of subtriangular outline, with strong convexity posteriorly. Shallow sulcus originating about mid-length. Faint growth line impressions near anterior margin. Strong teeth supported by high, thin parallel dental plates extending anteriorly for nearly half of length. (Exteriors are unknown.)

MEASUREMENTS. BC 12670: (X1) length = 23 mm, (X2) width = 18·4 mm, (X3) position of maximum width = 16·5 mm, (X4) depth = 7·4 mm; length of dental plates = 11·4 mm (Pl. 11, fig. 22).

DISCUSSION. The material is inadequate for specific assignment, but may be conspecific with the poorly known *Porambonites filosus* M'Coy from nearby Knockmahon, Co. Waterford. *Porambonites* is a common genus in the TLF (Carlisle 1979) and is currently under revision by Parkes & Harper. Significant differences, however, appear between this species and the older one in size, outline and internal morphology.
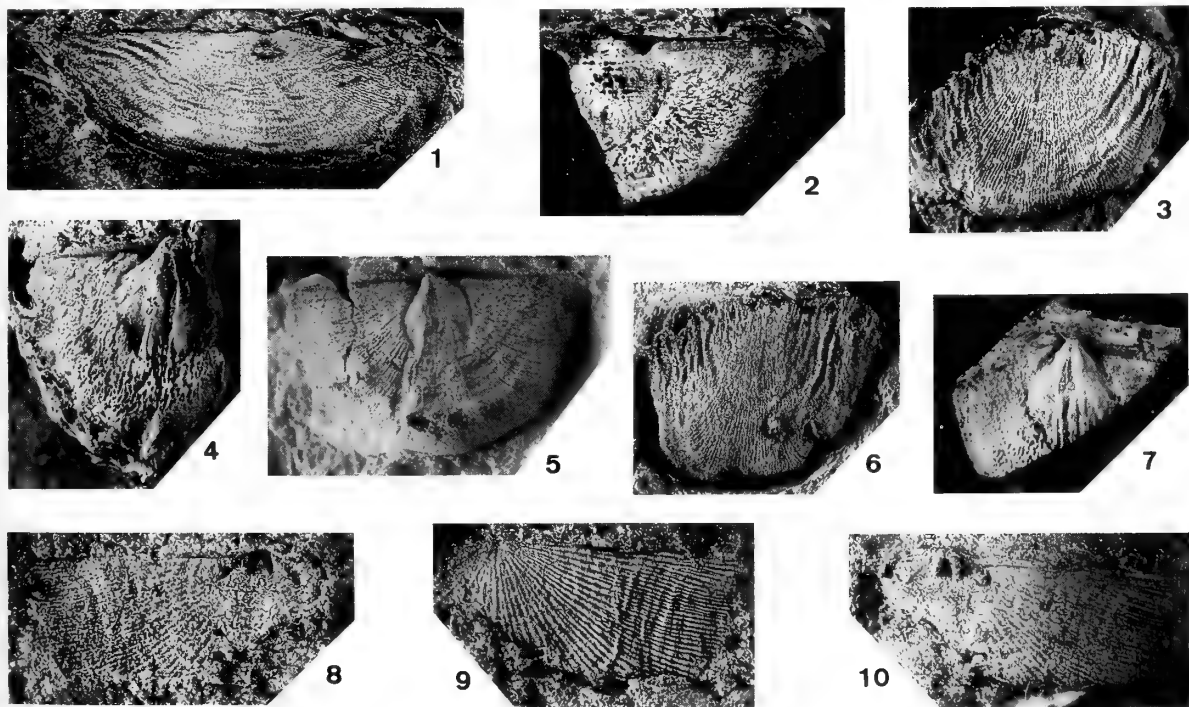
PLATE 15
Figs 1–7 *Leptaena* sp. Figs 1–4, 6–7, Kildare, Grange Hill Horizon 1. **1**, BC 12800, external mould of brachial valve, × 2. **2**, BC 12801, internal mould of pedicle valve, × 2. **3**, BC 12802, external mould of brachial valve, × 2. **4**, BC 12803, internal mould of pedicle valve, × 2. **6**, BC 12804, external mould of brachial valve, × 2. **7**, BC 12805, internal mould of pedicle valve, × 2. **Fig. 5**, Kildare, Grange Hill House Cottage, BC 12806a, internal mould of pedicle valve, × 2.
Figs 8–10 *Hibernodonta*? sp. Single specimen from Kildare, Grange Hill House Cottage. **8, 10**, BC 12807a, internal mould of brachial valve, and latex cast, × 4. **9**, BC 12807b, counterpart external mould of brachial valve, × 4.

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PLATE 16

Figs 1–7, 9–10 *Echinosphaerites* cf. *granulatus* M'Coy. Figs 1, 3–5, 7, 9–10, Carrigadaggan. 1, EE 134, slab with 2 flattened thecae, × 0·5. 3, EE 136, external mould of several plates, × 6. 4, EE 137, internal mould of several plates, × 4. 5, EE 138, external mould of several plates, × 4. 7, 10, EE 140, flattened theca with oral projection, and top view of same, × 2. 9, EE 141, internal mould of theca with oral projection, × 2. Figs 2, 6, Kilbride. 2, EE 135, internal mould of single plate, × 7. 6, EE 139, internal mould of single plate, × 8.

Figs 8, 11–18 Cheirocrinid, gen. et sp. indet. Figs 8, 11, Carrigadaggan. 8, EE 142, × 10. 11, EE 143, × 6. Figs 12–18, Kilbride. 12, EE 144, × 7. 13, EE 145, oral plate, × 10. 14, EE 146, oral plate, × 8. 15, EE 147, oral plate, × 10. 16, EE 148, × 7. 17, EE 149, × 7. 18, EE 150, × 9.

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A synopsis of neuropteroid foliage from the Carboniferous and Lower Permian of Europe

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CONTENTS

SYNOPSIS. The form-genus *Neuropteris* was initially established for compound leaves or fronds, whose pinnules had a constricted base and a non-anastomosed venation, and which are mainly found in the Carboniferous. Using a combination of frond/leaf architecture and cuticular features, it is now possible to divide this artificial taxonomic concept into nine more closely circumscribed and homogenous form-genera: *Neuropteris sensu stricto*, *Laveineopteris*, *Macroneuropteris*, *Margaritopteris*, *Neuralethopteris*, *Neurocallipteris*, *Neurodontopteris*, *Paripteris* and *Sphenoneuropteris*. In the palaeobotanical literature of the last half century (since 1940), fifty-seven adequately circumscribed species have been identified from Europe as belonging to *Neuropteris* in its traditional, broad sense (a further forty-four species names have been used, but are either based on inadequate type specimens, or have proved to be later synonyms of other species). Of these fifty-seven 'good' species. fifty-one can be assigned with reasonable confidence to one or other of the nine form-genera mentioned above. That the classification provides a reasonably robust expression of the natural relationships of the species is suggested by the fact that competition appears to have been greater between species of the same form-genus than between species of different form-genera. It is possible to correlate the distribution of some of these form-genera with the palaeoclimatic model that has been proposed based on coal ball evidence. For instance, *Neuropteris sensu stricto* and *Neuralethopteris* appear to have belonged to plants that favoured slightly wetter conditions within Carboniferous equatorial swamps. *Laveineopteris*- and *Paripteris*-bearing plants seem to have been less environmentally constrained, although a change between wetter and drier conditions seems to correlate with a change in the species present. The group as a whole seems to have been most diverse in the peat-accumulating swamps of the Carboniferous equatorial belt, but with clear differences in the

species present in the paralic and intra-montane basins. In the higher southern palaeolatitudes of Gondwana, the group is absent. In the higher northern palaeolatitudes of Angara and Kazakhstania it is also largely absent, with the exception of some possible paripterid species.

INTRODUCTION

The study of Upper Carboniferous palaeobotany in Europe has tended to follow two distinct lines, which may be summarized as coal ball studies and adpression studies. In recent years, the coal ball petrifactions have attracted most attention, and have yielded considerable information on the anatomy and thereby the affinities of the plants. The importance of this work is indisputable, but coal ball fossils can only give a partial view of the Late Carboniferous equatorial vegetation. For one thing, they only preserve plants that grew in the peat-accumulating habitats. Although this was the commonest habitat in the swamps, the acidic, water-logged substrate was normally low in oxygen and nutrient, which restricted the variety of plants it could support. Also, coal balls only formed where sea water could percolate through the peat deposits (Scott & Rex 1985). Where the peats formed in a lower delta plain setting (e.g. eastern North America, the Ukraine) there can be a good record of coal balls, but in middle or upper delta plain settings, or intra-montane basins, they are absent. Over much of Europe, coal balls are restricted mainly to just one coal seam in the lower Langsettian, with only a very few other known examples in the Yeadonian, upper Langsettian and topmost Duckmantian (this is excluding the silicified limnic peats in the Stephanian and basal Permian of southern France). For a general review of coal ball distribution, see Phillips (1980).

Of much wider occurrence in the European Upper Carboniferous are plant adpressions. These preserve quite a different part of the equatorial vegetation – mainly that growing on the raised levee banks within the swamps. Although forming a much smaller proportion of the original biomass, taphonomic bias has caused them to dominate the adpression record (Gastaldo et al. 1989). Also, because the edaphic conditions were not as extreme, the levees supported a much more diverse vegetation than the peat-accumulating habitats.

The abundance and diversity of the adpression assemblages gives them considerable potential significance for understanding the Late Carboniferous tropical vegetation, but there are a number of widely-perceived drawbacks. The majority of identifiable adpressions are fragments of foliage with (except in some ferns) little direct evidence of reproductive structures. Most 'angiospermocentric' neobotanists give such foliar organs a low taxonomic status, and this attitude has tended to rub off on palaeobotanists ('One good fertile specimen of a given species will tell far more than any quantity of sterile ones' – Andrews 1961). This viewpoint is given support by the traditional generic taxonomy developed by Brongniart (1822) for leaf fossils, and which is still being used in some quarters. It is based on pinnule morphology and venation, and is quite clearly artificial, often hiding natural relationships and differences between species. It ignores the fact that many of these Carboniferous leaves were architecturally complex structures, with many characters of potential phylogenetic value. By viewing them holistically and incorporating such details as leaf architecture into their taxonomy, a far more robust and natural classification can be developed (e.g. Gothan 1941, Laveine 1967, Zodrow & Cleal 1988, Cleal & Shute 1991a).

Another perceived difficulty with studying Upper Carboniferous adpressions is that they show little anatomical detail. Up to a point, this is a valid criticism, at least when compared with the quality of information that can be determined from coal ball petrifactions. However, it should be remembered that in many other parts of the geological column petrifactions are absent or rare. It has nevertheless been possible to determine many anatomical details from adpressions, particularly of the epidermis through cuticle studies (e.g. Thomas & Masarati 1982, Kerp 1991). Because of taphonomic factors, such as post-mortal tectonic deformation, cuticles are not as easy to prepare from Carboniferous adpressions as they often are from Mesozoic material. Nevertheless, they can sometimes be obtained from Carboniferous foliage fossils, providing data that can be of considerable taxonomic importance (e.g. Barthel 1961, 1962, Cleal & Zodrow 1989, Cleal & Shute 1991a).

The present paper brings together the results of the authors' studies on one particular group of adpressions which are particularly abundant in the Upper Carboniferous of Europe: fragments of pteridospermous fronds that were traditionally assigned to the form-genus Neuropteris Brongniart, and now referred to as neuropteroid fronds. By combining evidence of frond architecture (e.g. Gothan 1941, Laveine 1967, Zodrow & Cleal 1988, Cleal & Shute 1991a) and epidermal structure (Barthel 1961, 1962, 1976, Cleal & Zodrow 1989, Cleal & Shute 1991a, 1992), a revised generic classification of the fossils was introduced by Cleal et al. (1990). The first goal of the present study was to test the robustness of this classification. This was done by checking every species that has been recorded from Europe in the last half century, to see what proportion can be assigned to the more natural form-genera in the Cleal et al. classification.

As a by-product of doing this check, we have built up a database of the geographical and temporal distribution of species in each of the genera. This has allowed us to see if any patterns can be elucidated, which may have palaeogeographical or palaeoclimatic significance. Such distributional work is not novel in the Carboniferous (see Cleal 1991 for a review). However, by looking at the species distributions in the context of more natural form-genera, it is believed that more meaningful patterns will be revealed.

These fronds mostly belong to the order of plants known as the Trigonocarpales (sometimes also referred to as the Medullosales). The order, which is only known from the lowland, palaeoequatorial deposits of the Carboniferous and Lower Permian, consisted mainly of shrubs and small trees, although one small liana-like species has recently been described by Hamer & Rothwell (1988). They characteristically had large dissected leaves or fronds, sometimes up to 7 metres long (Laveine 1986), but more typically 1–2 metres long (e.g. Cleal & Shute 1991a). In addition to the form-genera covered by the present study, other trigonocarpalean fronds include Odontopteris (Brongniart) Sternberg, 1825,

1 metre

ion Bernhardi, 1800 (see Cleal & Shute 1991b), *Callipteridium* (Weiss) Zeiller, 1888a, *Alethopteris* Sternberg, 1825, *Lonchopteris* Brongniart, 1828, *Linopteris* Presl, 1838, and *Reticulopteris* Gothan, 1941. Traditionally, it has been assumed that both the ovuliferous and microsporangiate fructifications were attached directly to the vegetative fronds, and a number of examples showing this have been described in the literature (e.g. Dix 1932, Darrah 1937, Zodrow & McCandlish 1980). However, there has recently come to light evidence that in some of the trigonocarpaleans they formed more or less complex strobilus-like structures, attached either in an axillary position to the frond, or directly to the cauline axis (Drinnan *et al. 1990*, Laveine *et al.* 1991). The individual ovules were often large, robust structures, up to 8 cm long (Gastaldo & Matten 1978), which probably relied on flotation for dispersal. The microsporangia clusters, on the other hand, were mainly small delicate structures, containing either monolete or (in the Potonieaceae) trilete prepollen (Millay & Taylor 1979).

The group is not just important as a numerically significant component of the Trigonocarpales (at least as represented in the fossil record). Many species in the neuropteroid complex have proved stratigraphically useful. Preeminent is *Neuropteris ovata*, the base of whose range is the main index to the base of the Westphalian D stage, but many others also play an important role; in the biostratigraphical classification of Carboniferous strata outlined by Cleal (1991), 2 zones and 6 subzones are named after neuropteroid species. It is thus important to the biostratigrapher as well as the evolutionary palaeobotanist to place the taxonomy of these fronds on a firm footing.

METHODS

This analysis has been based on data extracted from palaeobotanical literature published over the last half century. A starting date of 1940 was chosen as providing both a realistic volume of literature to search, as well as an almost complete cover of geographical areas yielding plant fossils in Europe. In certain areas where there has been extensive work on Carboniferous palaeobotany, only the most recent monographs have been used, although where necessary they have been supplemented by other works which may document any species omitted from the monographs. Full details of this can be found below in the section 'Sources of data'.

Every neuropteroid species that has been identified from the Carboniferous and Permian of Europe during this half century has been assessed. It has then been either:

1. Assigned to one or other of the frond form-genera outlined below in the section 'Generic classification' and, where necessary, a new combination proposed; or
2. Assigned to the group of species that cannot be classified in one or other of the frond form-genera; or
3. Assigned to an earlier published species as a synonym, with brief reasons given, or a reference given to another authority, for the proposal; or
4. Assigned to the list of *nomen dubia* species, that were originally described on inadequate material.

The resulting taxonomic section of this paper thus includes for each species that is accepted as valid (1) its name, (2) a synonymy list (see further comments below), (3) reasons for generic assignment, (4) any other comments, and (5) its geographical and stratigraphical distribution.

Synonymy lists

The lists given are not complete and only include those references that are significant for defining the species: the basionym, the combination accepted in this analysis, where the type specimen(s) are published if they are not included in the protologue, and where there is a photographic record of the type specimen(s) if the original reproduction was an engraving or similar illustration. It also includes those species that have been published since 1940, which are now thought to be later synonyms.

In order to clarify the lists, they have been annotated using a system comparable to that outlined by Matthews (1973).

However, it has been found useful to add to the range of signs originally given by Matthews, and the full set as used here is listed below.

* The protologue of the basionym.
§ The valid publication of the combination accepted here.
T The type specimen(s) when not published in the proto-logue, or photographic illustrations of them if the original illustrations were poor.
? The inclusion of this reference is provisional due, for instance, to poor illustration.
. The present authors accept responsibility for including this in the synonymy; if a species is included as a synonym without the '.', then it is based on another authority, which is quoted at the end of the reference.
v The authors have seen the specimens in question.

Statistical analyses

The database built up as a result of this review has been subject to statistical analysis, to try to determine distributional patterns. Univariate and bivariate statistics were calculated using the Arcus Pro-II package (version 2). The statistics are straightforward and require little explanation other than that the method of least-squares was used in the regressions.

Cluster analyses were performed using the MVSP package, on an IBM PC-AT computer. This package is particularly useful, as it provides a routine (SORTDATA) for showing which species cause the clusters to form. Jaccard's Coefficient was used for the measure of similarity between assemblages, as this gives no weight to cases where a particular species is absent from both samples (Sokal & Sneath 1963). This was deemed preferable to measures such as the Simple Matching Coefficient, which takes such double-absences of a species into account, and which might distort the results with localities which have been only incompletely sampled. Clustering was performed using the unweighted pair group strategy, which on the whole tends to give a better resolution of the clusters in binary data than the mathematically simpler single linkage strategy (Sokal & Sneath 1963). A detailed discussion of the relative merits of the various similarity measures and clustering strategies available can be found in Sokal & Sneath (1963) and Everitt (1980).

It is widely recommended (e.g. Sneath & Sokal 1973) that similarity measures of this type should be investigated using both cluster and ordination methods. To this end, the matrices of Jaccard's Coefficients were submitted to Gower's Principal Coordinates Analysis (PCO), again using the MVSP package, which provides a series of two-dimensional graphical plots. The results generally confirmed the patterns observed using the cluster analysis, but did not have the merit of such a concise graphical presentation. As they add nothing to our conclusions, the results of these PCO analyses have not therefore been included in the paper.

The cluster analyses were performed on matrices of binary (presence/ absence) data for the various areas. Our information was not really amenable to establishing quantified values for the abundance of the species in the different areas. In any case, it has recently been shown that such presence/absence data in fact produce better results than quantified data in establishing patterns of geographical distributions of plant fossils, even where the quantified data can be reliably measured (Boulter *et al.* 1993).

GEOLOGICAL BACKGROUND

Chronostratigraphical terminology

This paper is not intended as a biostratigraphical analysis. The stratigraphical data is included only as a general guide and is limited to the distribution between stages. For brevity, the stage names have been abbreviated using a similar scheme to that used by Harland *et al.* (1982). Unfortunately, however, Harland *et al.* only used the European stages for the Visean and Namurian; for the higher part of the Carboniferous and the Permian, they switched to the Russian classification. We are therefore proposing a list of abbreviations for the full set of European stages, as summarized in Fig. 2. This figure also gives an estimate of the duration of each of the stages, based on the radiometric data summarized by Leeder (1988), and which includes the dates derived from sanidine crystals from tonsteins.

Sources of data

The following provides a summary of the areas into which the geographical distributional data have been divided, with a statement as to the sources from where the palaeobotanical information has been extracted. The locations of these areas are plotted in Fig. 3 on a palaeogeographical map for the Upper Carboniferous, using the same numbering of the areas as given below. The chronostratigraphical range of strata that yield plant fossils in each of the areas is shown using the abbreviations mentioned above. Some areas where strata of an appropriate age are known to occur will not be found below. These include the Campine Basin of Belgium, the Flöha Basin of southern Germany, the North Sudetic Basin of the Czech Republic, the Reşiţa and Sviniţa basins in Romania, and the various basins in the Balkans. They have been excluded from this analysis because the literature on the plant fossils is inadequate and/or more than 50 years old.

1. South-West UK (Arn–Can). The British records have been divided between those south and north of the Wales-Brabant Barrier. Those from the south belong mainly to what Calver (1969) called the South-West Basin, and refers to the South Wales, Forest of Dean and Bristol-Somerset coalfields (it excludes the Kent Coalfield, which is part of the Franco-Belgian Basin). The records of neuropteroid species is based mainly on the illustrations in Crookall (1959), although his taxonomy has needed considerable modification (partly done by Laveine 1967). Some additions have also been made following the biostratigraphical analysis of the Welsh fossils by Cleal (1978).

2. Pennines (Asb–WeD). This is taken in a wider sense than originally envisaged by Calver (1969), and includes both his Pennines and Scottish basins. Records of plant fossils from Scotland are relatively few but those that there are seem to differ little from those of the Pennines. The main source of data on the neuropteroid species in this area is Crookall (1959).

3. Franco-Belgian Basin (Pnd–WeD). This includes the Nord-Pas-de-Calais Coalfield in northern France, and the Mons-Charleroi-Namur Coalfield in Belgium (it also includes the Kent Coalfield in Britain, but there are few illustrated records of plant fossils from there). Neuropteroid species

Subsystems	Old Stages	Old Sub-Stages	New Stages	Stage Abbreviations	Duration of Stage in million years
Lower Permian	Autunian		Autunian	Aut	2(?)
Upper Carboniferous	Stephanian	Stephanian C	Stephanian C	StC	1
		Stephanian B	Stephanian B	StB	2
		Stephanian A	Barruelian	Bar	2
			Cantabrian	Can	1
	Westphalian	Westphalian D	Westphalian D	WeD	2
		Westphalian C	Bolsovian	Bol	3
		Westphalian B	Duckmantian	Duc	2
		Westphalian A	Langsettian	Lan	2
	Namurian	Namurian C	Yeadonian	Yea	1(?)
		Namurian B	Marsdenian	Mrd	2
			Kinderscoutian	Kin	2
Lower Carboniferous		Namurian A	Alportian	Alp	1
			Chokierian	Cho	2
			Arnsbergian	Arn	2
			Pendleian	Pnd	2
	Visean		Brigantian	Bri	4(?)
			Asbian	Asb	5(?)

Fig. 2 Stratigraphical schemes for the strata known to yield neuropteroid fossils. It includes the Heerlen set of stages and substages, the set of stages currently accepted by the IUGS Subcommission on Carboniferous Stratigraphy, and a newly-revised set of abbreviations for the stages. Also given is the estimated duration of each stage, based mainly on Leeder (1988).

have been documented better in these coalfields than probably anywhere else in the world. This is mainly due to the monographs by Stockmans (1933) and, perhaps more significantly, by Laveine (1967). Additional data have also been taken from Stockmans & Willière (1953, 1955), van Amerom & Lambrecht (1979) and Paproth et al. (1983).

1. S. Limburg (Lan–Bol). This lies between between the NW Germany basin and the Kempe Basin of Belgium. There have been few studies on the palaeobotany of this basin in recent years, the only ones with illustrations of neuropteroid taxa being by Jongmans (1953a, 1953b, 1954). In order to attempt a more comprehensive assessment of the fossils from here, data has also been incorporated from Jongmans & Gothan (1915).

2. NW Germany (Arn–WeD). This area is based mainly around the Ruhr Coalfield, but also includes the smaller coalfields in the Osnabrück Highlands (Ibbenbüren, Piesberg and Hügel), which appear to belong to the same basin (Josten et al. 1984). The most recent monograph on the neuropteroid taxa from here is by Gothan (1953) and most of the records quoted herein are based on this analysis. Additional records have been taken from Josten (1983, 1991) and Josten & Laveine (1984).

3. NE Germany (Kin–Bol). This is part of the paralic basin that has been discovered in deep boreholes in the region of Rostock, on the northern coast of what used to be the German Democratic Republic. Plant fossils from the Namurian have been documented by Kahlert (1979). The

first illustrated records of plant fossils from the Westphalian were by Daber (1963a, 1967), but the stratigraphical information provided is not sufficiently detailed for the purposes of this study. More detailed evidence has recently been provided by Gründel (1992) and Kahlert (1992), and have been used as the basis of the records incorporated in this study. The claims that the upper part of this sequence extends up into the Westphalian D or even Stephanian (e.g. Kahlert 1992) are based on doubtful evidence such as the presence of conifer remains and is not accepted here.

7. Lublin (Asb–Bol). This represents the easternmost extension of the belt of paralic deposits that extended across northern Europe; the highest marine strata known here can be correlated with what is known as the Vanderbeckei Marine Band in Britain, and marks the boundary between the Langsettian and Duckmantian stages. The best documentation of neuropteroid foliage from here is by Migier (1966), but there are also useful but unillustrated summaries provided by Migier (1980) and Kotasowa & Migier *in* Bojkowski & Porzycki (1983).

8. Zwickau-Oelsnitz (WeD). This was an intra-montane basin formed in a small depression in present-day Saxony, SE Germany (Pietzsch 1962). The neuropteroid taxa from here have been documented by Daber (1955, 1957).

9. Saxony (Aut). This refers to the Erzgebirge (or Ore Mountains), Döhlener, Weißig and North Saxony Volcanic basins, which lie between the Saale Trough and the Central Bohemian Basin. They contain upper Stephanian and Rot-
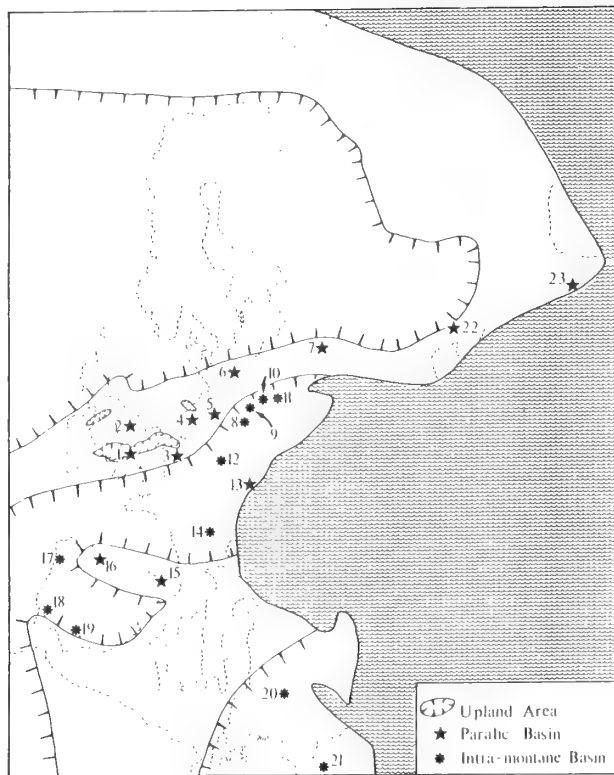
Fig. 3 Palaeogeographical map of Europe in the Late Carboniferous, showing location of areas that have yielded neuropteroid adpressions. Map based mainly on the Stephanian reconstruction of Scotese (1986), with modifications adapted from Bless *et al.* (1977) and Haszeldine (1984). The marine areas, both shelf and deep ocean, are shaded. Locality numbers: 1 – South-West United Kingdom; 2 – Pennines; 3 – Franco-Belgian Basin; 4 – S. Limburg; 5 – NW Germany; 6 – NE Germany; 7 – Lublin; 8 – Zwickau-Oelsnitz; 9 – Saxony; 10 – Upper Silesia; 11 – Intra-Sudetic Basin; 12 – Saar-Lorraine; 13 – Alps; 14 – Massif Central; 15 – Pyrenees; 16 – NW Spain; 17 – N. Portugal; 18 – S. Portugal; 19 – S. Spain; 20 – Svoge; 21 – Turkey; 22 – Donets; 23 – N. Caucasus.

liegende strata, although only the latter have yielded plant fossils. The degree to which the basins were originally connected is still not clear, but Barthel (1976) has shown that, from a floristic standpoint, they combined to form a more or less homogeneous unit. Barthel provides a brief account of the geology, together with a detailed documentation of the plant fossils.

10. Upper Silesia (Asb–WeD). This basin straddles the Polish-Czech border. The name comes from the Upper Silesia Coalfield in Poland (Bojkowski & Porzycki 1983), while in the Czech Republic it is represented by the Ostrava-Karvina Coalfield (Dopita & Havlena 1977). Up until the early Namurian, it was part of the paralic belt that stretched across northern Europe. Thereafter, however, marine influence ceased, and it became an intra-montane basin. The neuropteroid taxa from the Namurian and lower Westphalian of this basin are documented by Stopa (1957), Kotasowa (1968) and Purkyňová (1971). The upper Westphalian plant

fossils are less well documented, although some useful data is provided by Kotasowa (1979).

11. Intra-Sudetic Basin (?Asb–Aut). This also straddles the Polish-Czech border. Traditionally, it was taken to include the Lower Silesia, Podkrkonoší and Poorlická pánev coalfields. However, sedimentological work summarized by Holub *et al.* (1977) suggests that it was part of a larger area of sedimentation, also including the large Central Bohemian 'basin', as well as smaller areas of outcrop such as the Boskovice and Blanice furrows (see also comments by Havlena 1953 and Wagner 1977). It is in this wider sense that we use the term Intra-Sudetic Basin. Most of the neuropteroid taxa are documented by Němejc (1949) and Havlena (1953).

12. Saar-Lorraine (Duc–WeD, Bar–Aut). This was an intra-montane basin, lying between the Rheno-Hercynian and Saxo-Thuringian zones, and now straddling the Franco-German border. The deep borehole Saar-1 has proved that deposition started in the late Visean (Weingart 1976). However, the exposed part of the sequence, and that which has yielded virtually all known neuropteroid taxa, ranges from upper Duckmantian to Autunian, with a stratigraphical gap from the top Westphalian D to upper Baruellian. The neuropteroid taxa from here have been documented by Cleal (1985) and Laveine (1989), with additional contributions by de Jong (1974), Doubinger & Germer (1975a, 1975b), Boersma (1978) and Cleal & Zodrow (1989). Also, although it was published before the starting point that we have selected for this study, the exceptionally illustrated monograph by Bertrand (1930) cannot be ignored (although his species have not been included in the synonyms).

13. Alps (?Cho–Aut). Caught up in the complex tectonic deformation of the Alps are numerous patches of Carboniferous strata yielding plant fossils. The heavy tectonism means that the fossils are on the whole fragmentary and yield no cuticle. Also, the dislocation of the strata means that it is often difficult to place them in any sort of coherent stratigraphical continuum. Nevertheless, enough material has been collected over the years to allow many neuropteroid species to be recognized from the Austrian (Fritz *et al.* 1990), Swiss (Jongmans 1960) and French (Greber 1965) alps. Most material comes from the less tectonized Internal Zone (also known as the Briançonnais Zone in France), although some material has also come from the External Zone.

14. Massif Central (Can–Aut). Within this upland area in France lie a series of mainly small, intra-montane basins that developed during the Stephanian as a result of Variscan tectonic activity. The most important include St. Étienne (the eponymous area for the Stephanian Series), Autun (the eponymous area for the Autunian Stage), Commentry, Brive, Blanzy, Bert, Decize and Decazeville; a more complete list is provided by Doubinger & Vetter (1985). The definitive work on the plant fossils of this area is Doubinger (1956), who reviewed and partially documented the upper Stephanian and basal Permian palaeobotany of all of the major basins. The main drawback of this work is that she persisted in using a number of species described originally by Zeiller (1888a, 1906), despite the fact that the types are totally inadequate and Doubinger herself had no new material. As a consequence, some of these Zeiller species, which otherwise would not have been included, have had to be referred to in this analysis. Other major monographs on the palaeobotany of

individual basins are by Vetter (1968 – Decazeville) and Langiaux (1984 – Blanzy).

15. Pyrenees (Kin, Aut). Like the Alps, this area has been subjected to considerable tectonic deformation. Terrestrial Upper Carboniferous and Lower Permian strata occur in a number of small, isolated basins, and plant fossils are widely distributed. However, there are few illustrated records of them in recent years, the only significant exceptions being by Delvolvé & Laveine (1985 – Kin) and Broutin & Gisbert (1985 – Aut).

16. NW Spain (Mrd–Aut). This is an area of Upper Palaeo-zoic deposits that ranges over parts of Asturias, Palencia and León, and is sometimes referred to as the Cantabrian Zone. It was subjected to major disruption by Variscan tectonics, resulting in sequences containing several angular unconformi-ties, and preserved in a series of disjointed outcrops. Mainly through the work of Wagner and his collaborators, the complex geology has been at least partly unravelled. Wagner (1970) and Wagner & Winkler Prins (1985) provide valuable summaries, and more detailed information can be found in Truyols *in* Martinez Diaz (1983). As part of this work, extensive collections of plant fossils have been made. Up to the late Westphalian D, deposition was mainly marine, with only intermittent fluvio-deltaic incursions, but at higher levels non-marine strata become increasingly predominant. Conse-quently, the Marsdenian to Bolsovian plant fossil record is patchy, but from the Westphalian D upwards it is effectively continuous into the Permian. General reviews of the plant fossils are provided by Wagner (1959, 1962, 1966) and Stockmans & Willière (1965), but none are complete. They have therefore been supplemented by the records from individual coalfields: Central Asturia (Jongmans 1952a, Wag-ner 1971, Wagner & Alvarez-Vázquez, 1991), San Emiliano (Moore *et al.* 1971), Cervera de Pisuerga (Wagner 1960, Cleal 1981), Tejerina (Wagner *et al.* 1969), Guardo (Wagner *et al.* 1983), Ciñera-Matallana (Wagner 1963, 1964), and Sabero (Knight 1983). Also, an undocumented list of Stephanian C fossils by Wagner & Laveine *in* Wagner & Martínez García (1982) has been included, being the only recent record from strata of this age.

17. N. Portugal (WeD, StC–Aut). Most of the Upper Car-boniferous and basal Permian in Portugal occurs in the north of the country, near Oporto (Sousa & Wagner 1983). They represent isolated intra-montane basins in the Central Iberian tectonic zone, and according to Wagner (1983a) can be related to the Carboniferous deposits in S. Spain (see below). Of those containing Westphalian strata, only that at Ervedosa has yielded abundant plant fossils, including neuropteroid fronds. The other basins rich in plant fossils (the Douro and Buçaco basins) are Stephanian C to Autunian in age. The palaeobotany of these deposits is reviewed by Wagner & Sousa (1983).

18. S. Portugal (WeD). This refers to three small outliers that are the only development of continental Upper Carbon-iferous rocks in southern Portugal. They are the remains of an elongate basin (the Santa Susana Basin) that developed along the fracture-zone that separates the Ossa-Morena and South Portuguese tectonic zones. Much of the sequence is conglomeratic, but there are also coals with finer-grained clastic deposits that have yielded plant fossils. The latter are reviewed by Wagner & Sousa (1983).

19. S. Spain (Lan, StC–Aut). Carboniferous and Permian terrestrial deposits in the southern half of the country are very patchy, being mainly restricted to small, fault-bounded basins. Westphalian plant fossils have been recorded from just two areas: the Villaneuva del Rio y Minas Coalfield in Sevilla (Lan – Wagner *et al.* 1983), and Peñarroya-Bélmez-Espinez (or Guadiato) Coalfield in Cordoba (Wagner 1983a, 1983b, 1990). A third area of Westphalian strata occurs in the Sierra de San Pedro in Cáceres (Wagner 1983a), but there appear to be no records of plant fossils from here.

From higher strata, the best documented assemblages of plant fossils occur near Guadalcanal in northern Sevilla (Broutin 1986) and the Puertollano Coalfield in Ciudad Real (Wagner 1985), In addition, there are records from Henare-jos in Cuenca (Wagner *et al.* 1985). Plant fossils have been reported in a number of other outcrops of Autunian strata (reviewed by Wagner & Martínez García 1982, and Martinez Diaz 1983), but none have yielded neuropteroid foliage.

20. Svoge (?Pnd–?Cho; Yea–Bol). This is the most impor-tant coalfield in Bulgaria, and represents the remains of an intra-montane basin (Tenčov 1971). The most comprehensive analysis of the Carboniferous plant fossils from here is by Tenčov (1977). Another major coalfield, known as the Dobroudja Basin, has been discovered in eastern Bulgaria below Mesozoic cover (Tenčov & Koulaksuzov 1972) but to date the plant fossils have not been monographed. The palaeobotany of the small upper Stephanian and Permian basins in northwest Bulgaria (Tenčov 1971, 1973) have also not been revised taxonomically in recent years.

21. Turkey (Yea–WeD). Upper Carboniferous occurs in a number of small outcrops near the northern coast of Turkey, the most important being near Zonguldak, Amasra, Pelitova and Azdavay. The stratigraphy is summarized by Kerey *et al.* (1986), who also provide a well documented record of the plant fossils. A more extensive listing of fossils is provided by Jongmans (1955), but is unillustrated and so cannot be judged.

22. Donets (Bri–Aut). The Donets Basin lies on the south-ern edge of the Russian Platform, and has produced the most important coalfield in eastern Europe. Brief accounts of the Upper Palaeozoic geology of the area are given by Kler *et al.* (1975) and Aizenverg *et al.* (1975). Prior to the very late Visean, it was exclusively an area of marine-carbonate depo-sition. From the Brigantian, however, deltaic complexes frequently extended into the basin, and the rest of the Carboniferous consists of alternating marine and non-marine deposits. This has given the basin considerable potential importance for correlating the so-called Heerlen chronostrati-graphical classification, that was based on the non-marine sequences of western Europe, and the standardized Russian chronostratigraphy, based mainly on the marine sequences of the Moscow Basin (Wagner *et al.* 1979). The most detailed illustrated documentation of the plant fossils from here have been by Novik (1952, 1954, 1968), although additional unil-lustrated data are given by Fissunenko & Laveine (1984).

23. North Caucasus (?Kin–WeD, StB–StC). A number of areas of Carboniferous outcrop occur on the northern slopes of the Caucasus (Kavkaza) Mountains in Georgia. Their geology is outlined by Pogrebnov (1975) and Kler *et al.* (1975). Mainly Tournaisian marine deposits are overlain unconformably by exclusively non-marine Upper Carbonifer-

ous deposits. They are of interest as the easternmost Carbon-
iferous plant-bearing deposits of Laurasia, although their
assemblages are regarded as having close affinities with those
of western Europe, closer in fact than with the geographically
nearer Donets. The plant fossils from here are described by
Novik (1952, 1978), Shchegolev (1979) and Anisimova
(1979).

TAXONOMIC BACKGROUND

Criteria for accepting a species

Most of the species listed in the *nomen dubia* section of this
paper are validly published according to the International
Code of Botanical Nomenclature, but in our view have been
described from insufficient material to demonstrate the range
of morphological variation. A knowledge of this variation is
essential if a species is to be usable for specimens other than
the types, and thus for it to be a viable taxonomic entity
(Cleal 1986).

There are no fixed rules for determining if a species has
been adequately defined; common sense has to be the main
guide. If it is based mainly on isolated pinnules and short
fragments of pinna, then 'tens' of specimens are almost
certainly needed to demonstrate the variation. If, on the
other hand, the specimens represent large segments of pri-
mary pinna branches, then the variation may be demon-
strable with less than ten. Rarely, if ever, is a single isolated
specimen a sufficient basis for describing a new species, no
matter how different it may seem to be from existing species.

The generic model

The generic classification used here has been developed from
taxonomic schemes proposed by Gothan (1941), Laveine
(1967) and Cleal *et al.* (1990). Those of Gothan and Laveine
were based on features of gross morphology, primarily of
frond architecture, while Cleal *et al.* also used epidermal
evidence. In this study, we have also used three other, less
well-known form-genera (*Neurodontopteris, Sphenoneuro-
pteris, Margaritopteris*) to accommodate a small number of
species, which would otherwise be unassignable. The main
diagnostic characters for each form-genus is summarized in
Table 1. In the following section, the systematics of each
form-genus is briefly summarized. It should be emphasized
that an attempt has been made to make these form-genera as
far as possible natural clusters of species, and are thus
form-genera in the sense of Cleal (1986) and Visscher *et al.*
(1986), rather than in the artificial sense given in the Interna-
tional Code of Botanical Nomenclature.

Form-genus *LAVEINEOPTERIS* Cleal, Shute & Zodrow (1990: 489)

TYPE. *L. loshii* (Brongniart) Cleal, Shute & Zodrow

COMMENTS. This was established for the neuropteroid spe-
cies that have been shown to have large, orbicular cyclopterid
pinnules in the lower part of the frond (Figs 4, 5). Such
cyclopterids have often been taken to characterize all of the
imparipinnate neuropteroid species. As pointed out by Cleal
& Shute (1991a), however, cyclopterids are only known

Fig. 4 *Laveineopteris loshii* (Brongniart) Cleal *et al*. Copy of von
Roehl (1868: fig. 17), showing orbicular cyclopterids attached
near the dichotomy of the primary rachis. Origin: Hibernia
Colliery, near Gelsenkirchen, the Ruhr, Germany. Here
reproduced at × 0·28 of original specimen.

attached to a very small range of species, all of which also
show a distinctive set of cuticular characters, such as the
virtual absence of intercellular flanges on the abaxial pinnule
surface, the absence of multicellular trichomes, and the weak
differentiation of the costal and intercostal fields of the
adaxial pinnule epidermis (Fig. 17C,D).

It is important to emphasise that the laveineopterid cyclo-
pterids are different from the swollen pinnules present at the
base of the true neuropterid fronds. As pointed out by Cleal
& Zodrow (1989), these cyclopterid pinnules have a mark-
edly different epidermal structure from the 'ordinary' pin-
nules in the main part of the frond. Also, they were not
originally orientated in the same plane as the rest of the
frond. Their function is still unclear, but it is unlikely to have
been simply photosynthetic.

The presence of cyclopterid pinnules suggests that *Laveine-
opteris* is more closely related to the callipteridiums than the
neuropterids, since similar cyclopterids are known attached
to both *Callipteridium* and *Margaritopteris* (Laveine *et al.*
1977). Unfortunately, little is known of the epidermal struc-
ture of the callipteridiums to support this view.

The anatomy of the rachides is of a type usually associated

Table 1 The gross morphological and cuticular characters used to diagnose the form-genera covered in this paper. Expanded from Cleal & Shute (1992: Table 1).

	Laveineopteris	Neuropteris	Macroneuropteris	Neurocallipteris	Neuralethopteris	Paripteris	Neurodontopteris
Stomata on only abaxial surface (−) or both surfaces (+)	−	−	−	±	−	−	+
Costal and intercostal cells on adaxial surface different (+) or similar (−) from one another	−	+	−	+	+	−	+
Abaxial cuticle with strong (+) or virtually no (−) anticlinal walls	−	+	+	+	+	−	+
Stomata anomocytic (An), brachyparacytic (Br), cyclocytic (Cy) or amphicyclocytic (Am)	An	An/Br	Br/Cy	Cy/Am	Br(?)	An(?)	Cy
Papillae on abaxial surface	−	+	+	+	+	−	+
Multicellular trichomes on abaxial surface	−	+	+	−	−	−	+
Orbicular or reniform cyclopterid pinnules in lower part of frond	+	−	−	−	−	−	−
Primary pinna branches bipinnate (2), tripinnate (3) or quadripinnate (4)	¾	¾	⅔	3	3	?	2
Pinnules that are normally partially fused to rachis except near base of frond	−	+	−	+	−	−	+
Midvein usually decurrent and extending for <⅔ pinnule length (+) or non-decurrent and extending for >⅔ pinnule length (−)	−	+	−	+	−	−	+
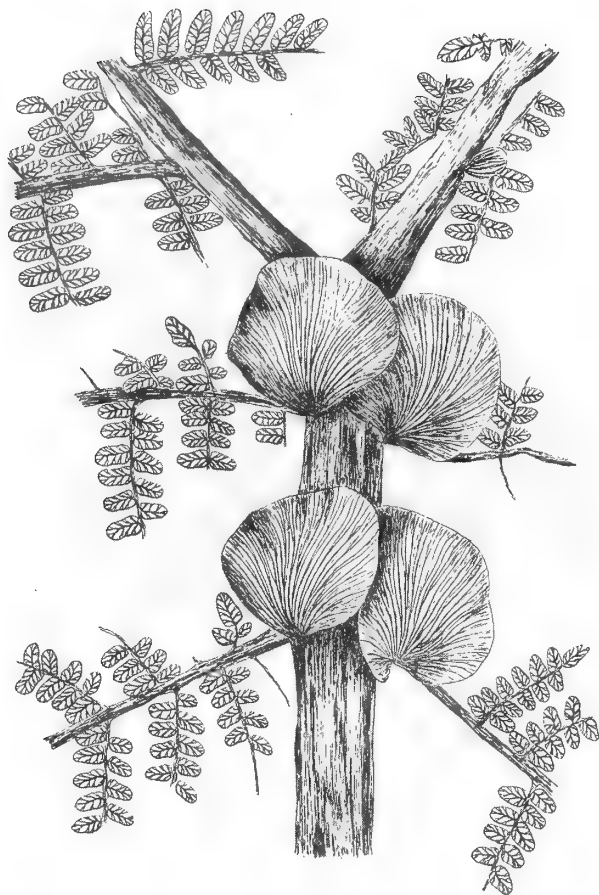
Fig. 5 *Laveineopteris rarinervis* (Bunbury) Cleal *et al*. Copy of Carpentier (1930: fig. 1), showing orbicular cyclopterids attached near the dichotomy of the primary rachis. Here reproduced at × 0·7 life size.

with the Trigonocarpales (Oestry-Stidd 1979). Little is known of the fructifications, other than that large ovules were attached directly to the frond, probably at the end of ultimate pinnae (Kidston 1904).

Form-genus *MACRONEUROPTERIS* Cleal, Shute & Zodrow (1990: 488)

TYPE. *M. macrophylla* (Brongniart) Cleal, Shute & Zodrow

COMMENTS. Most neuropteroid fronds have a dichotomy of the primary rachis producing tripinnate or occasionally quadripinnate branches. In some species, however, the dichotomy of the primary rachis produces less-divided, essentially bipinnate, primary rachis branches (Figs 6–7). These species also have a number of distinctive epidermal characteristics, such as brachyparacytic or cyclocytic stomata (Fig. 17E,F). It was for this distinctive group of species that Cleal *et al.* (1991) proposed the form-genus *Macroneuropteris*.

The fronds of *Macroneuropteris* are very similar to *Neuropteris sensu stricto*, except that they are less divided. Of particular significance is the presence in at least one macroneuropterid species (*M. scheuchzeri*) of so-called 'Odontopt-

eris lindleyana'- type pinnules (e.g. Crookall 1959: pl. 57, fig. 1), which can be compared with laciniate pinnules in the lower part of true neuropterid fronds (e.g. Stockmans 1933: pl. 11 fig. 1; pl. 12 fig. 2; Zodrow & Cleal 1988: pl. 4 fig. 3). There is no evidence of the orbicular cyclopterid pinnules of *Laveineopteris* or *Margaritopteris*.

Nothing is known of the fructifications. Beeler (1983) claimed that the rachis anatomy is of a type typical of the Trigonocarpales. However, this was based purely on evidence of association; she could find no such rachides with macroneuropterid pinnules directly attached.

Form-genus *MARGARITOPTERIS* Gothan (1913: 168)

TYPE. *M. coemansii* (Andrä) Gothan

COMMENTS. Most species included in this form-genus have broadly attached and/or lobed pinnules, and prior to Gothan's protologue were assigned to *Odontopteris* (Brongniart) Sternberg, 1825 or *Sphenopteris* (Brongniart) Sternberg, 1825 (see Laveine *et al.* 1977). However, one species, originally included in *Neuropteris* also belongs here ('*N.' multivenosa* Purkyňová). Laveine *et al.* (1977) have shown that it is almost certainly the ancestral form of *Callipteridium*. Nothing is known of the fructifications or stem/rachis anatomy.

Form-genus *NEURALETHOPTERIS* Cremer ex Laveine (1967: 97)

TYPE. *N. schlehanii* (Stur) Laveine

COMMENTS. This form-genus is used for alethopterid-like fronds, in which the pinnules have a constricted base (Fig. 8). Most of its component species were originally described as neuropterids, but they in fact have little to do with that form-genus in its currently defined sense.

The taxonomy of the form-genus has been thoroughly discussed by Laveine (1967), and need not be repeated. Our only disagreement with his analysis concerns the authorship of the taxon. Laveine quotes Cremer (1893), but this is a thesis that was not effectively published. Wagner (1963, 1965) suggested that the name should be resurrected, but provided neither a diagnosis nor type. The first validly published diagnosis is in fact in Laveine's study, who must therefore be taken as the author of the genus.

The architecture of the frond has been established with reasonable certainty by Laveine *et al.* (1992). As with most of the trigonocarpaleans, the frond had a dichotomy of the primary rachis producing two tripinnate primary rachis branches. Most significantly, there appear to be no intercalated elements on the primary rachis branches between the secondary pinnae. The lack of this feature separates *Neuralethopteris* from most of the other neuropteroid fronds and helps confirm that its affinities lies closest with the alethopterids.

There have been a number of reports of sporangial organs attached or closely associated with neuralethopterid fronds (Dix 1932, 1933; Arnold 1949; Jongmans 1954; Stockmans & Willière 1961; Laveine 1967). Dix and Arnold both referred them to the form-genus *Aulacotheca*, but Jongmans identified them as *Whittleseya*. By studying a range of specimens from a single locality, Stockmans & Willière concluded that this apparent taxonomic difference in fact reflected infraspecific
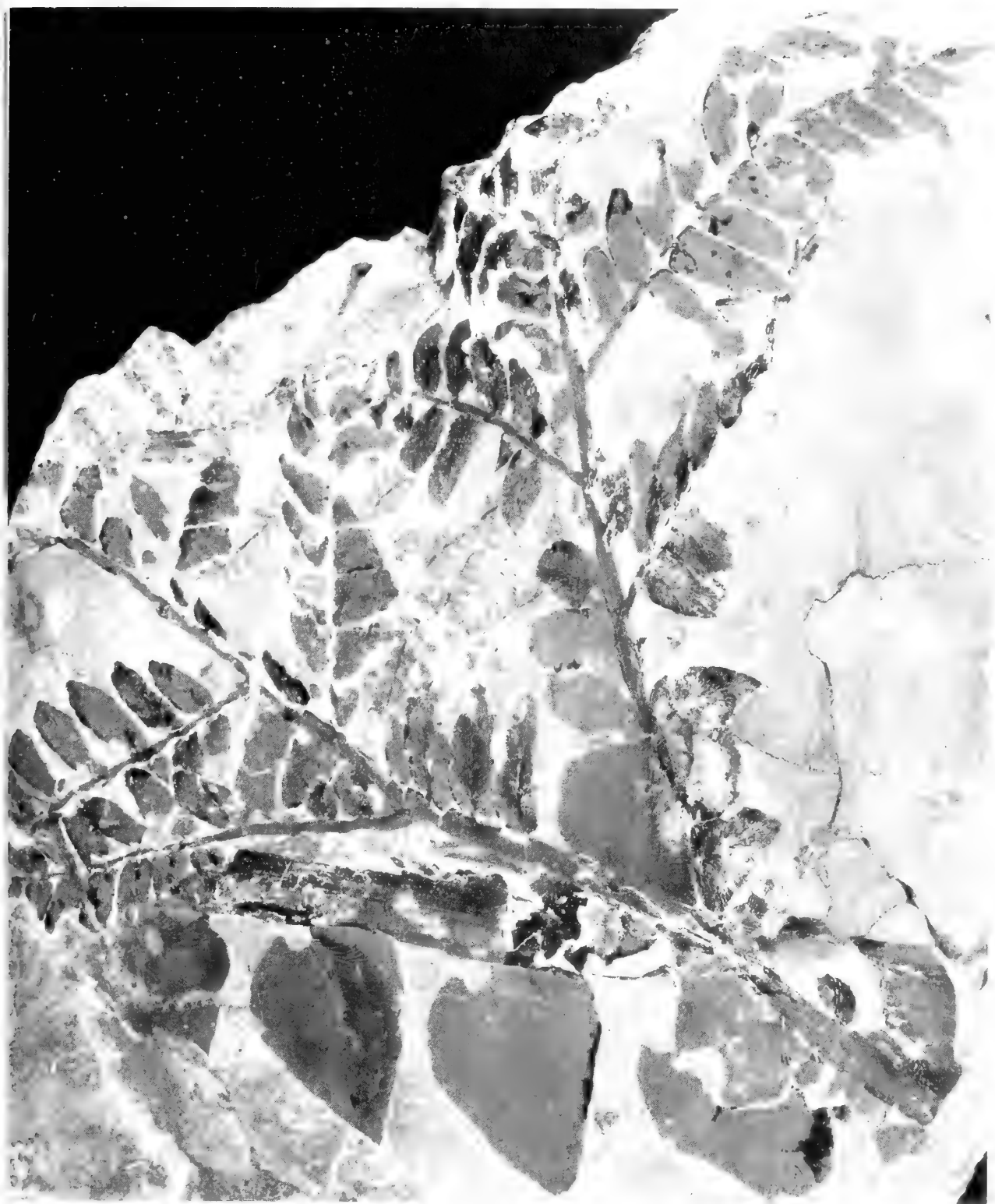
Fig. 6 *Macroneuropteris macrophylla* (Brongniart) Cleal *et al.* Specimen showing lower part of frond. V.2970. Westphalian D, Radstock, Somerset, UK. Natural size.
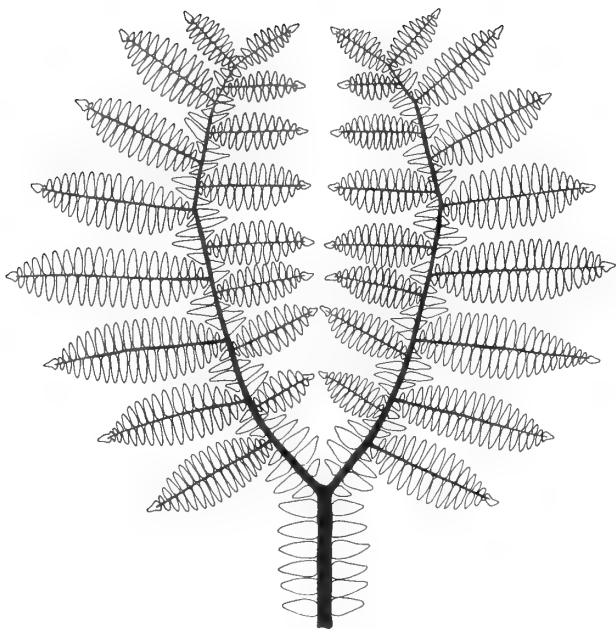
Fig. 7 Reconstruction of *Macroneuropteris* frond (*M. macrophylla* (Brongniart) Cleal *et al.*). Based on work done with Professor J.-P. Laveine.

morphological variation. They therefore proposed the form-genus *Givesia* for the neuralethopterid sporangial organs.

No ovules have been found attached to *Neuralethopteris* fronds, although Jongmans (1954) reported large, *Rhabdocarpus* ovules in close association. There is no available evidence of the stem or rachis anatomy.

Form-genus *NEUROCALLIPTERIS* Sterzel (1895: 283)

TYPE. *N. gleichenioides* (Stur) Sterzel (*Neuropteris gleichenioides* Stur).

COMMENTS. The systematic basis of this form-genus is given by Cleal *et al.* (1990). In essence, it refers to a group of Stephanian and Lower Permian neuropteroid fronds (Fig. 9), which have been shown to have more complex stomatal apparatuses than typical neuropterids (Fig. 10). Relatively little is known of the frond architecture but what information is available (e.g. Šetlík 1980) suggests that it is very similar to that of *Neuropteris sensu stricto*. However, as none of the species are that well known, the genus may not be fully homogeneous. Evidence of fructifications or stem/rachis anatomy is unknown.

In the upper Barruelian to Autunian is found a species which looks very like *Neurocallipteris*, but has an anastomosed venation. This was generally referred to as *Reticulopteris germarii* (Giebel) Gothan, but it is now assigned to a different form-genus, namely *Barthelopteris* Zodrow & Cleal (1993). Thus, just as *Reticulopteris* is the mesh-veined form of *Neuropteris*, and *Linopteris* is the mesh-veined form of *Paripteris*, *Barthelopteris* is the mesh-veined counterpart of *Neurocallipteris*.

Form-genus *NEURODONTOPTERIS* Potonié (1893: 124)

TYPE. N. auriculata (Brongniart) Potonié

COMMENTS. This form-genus was originally established for species showing pinnule characteristics intermediate between *Neuropteris* and *Odontopteris*. In this sense, it is clearly an artificial concept. However, there has been a recent reconstruction of the frond (Langiaux 1984: 105) from which a more 'natural' concept for the form-genus can be developed. Obvious characteristics include the smaller and less-divided frond compared with *Neuropteris* (Fig. 12) and the tendency of the pinnules to be fused to the rachis along the basiscopic side. Cuticular evidence also clearly characterizes the type species (described by Barthel 1976, under the incorrect name *Neuropteris cordata* – Z. Šimůnek, pers. comm. 1992). Distinctive features include the pinnules being amphistomatic and the cyclocytic stomata without marked papillae (Fig. 11). The form-genus is in clear need of revision and is used here only to include the type species. The frond architecture suggests affinities with the Trigonocarpales. However, there is no evidence of fructifications or stem/rachis anatomy to support this view.

Form-genus *NEUROPTERIS* (Brongniart) Sternberg (1825: xi)

BASIONYM. *Filicites* sect. *Nevropteris* Brongniart (1822: 233)

TYPE. *Neuropteris heterophylla* (Brongniart) Sternberg

COMMENTS. This name was originally established by Brongniart for all fossil frond fragments bearing pinnules with a constricted base and non-anastomosed venation. Subsequent work demonstrated that several clusters of species could be recognized in the traditional concept of *Neuropteris* (Gothan 1941, Laveine 1967, Cleal & Zodrow 1989) but it was not certain which of them included the type species (*N. heterophylla*) and thus was true *Neuropteris*. The problem was solved by the study of the cuticles and frond architecture of the type species by Cleal & Shute (1991a), and allowed the formal re-classification of the group by Cleal *et al.* (1990) (NB. the title of the Cleal & Shute 1991a paper was changed at the last minute and is different to that quoted in the bibliography at the end of Cleal *et al.* 1990). It is the emended concept of *Neuropteris* proposed by Cleal *et al.* (1990) that is used in this paper.

Despite previous preconceptions, *Neuropteris sensu stricto* has pinnules that are often partly fused to the rachis, and have a relatively weakly developed midvein (Fig. 13). Like *Laveineopteris*, the main dichotomy of the primary rachis produces tri- or rarely quadripinnate branches (Figs 14–16). Unlike *Laveineopteris*, however, there are no orbicular cyclopterids attached to the proximal part of the frond. Instead, the primary rachis below the dichotomy bears rachides with enlarged and/or laciniate pinnules attached. Both from their orientation relative to the rest of the frond, and their epidermal structures, these basal pinnules would seem to have simply been photosynthetic structures, not differing significantly in function from the pinnules higher in the frond.

During the middle Westphalian, *Neuropteris* developed progressively more flexuous veins, culminating in the Bolsovian in a fully anastomosed venation (Josten 1962, Zodrow & Cleal 1993). This anastomosed form of neuropterid is
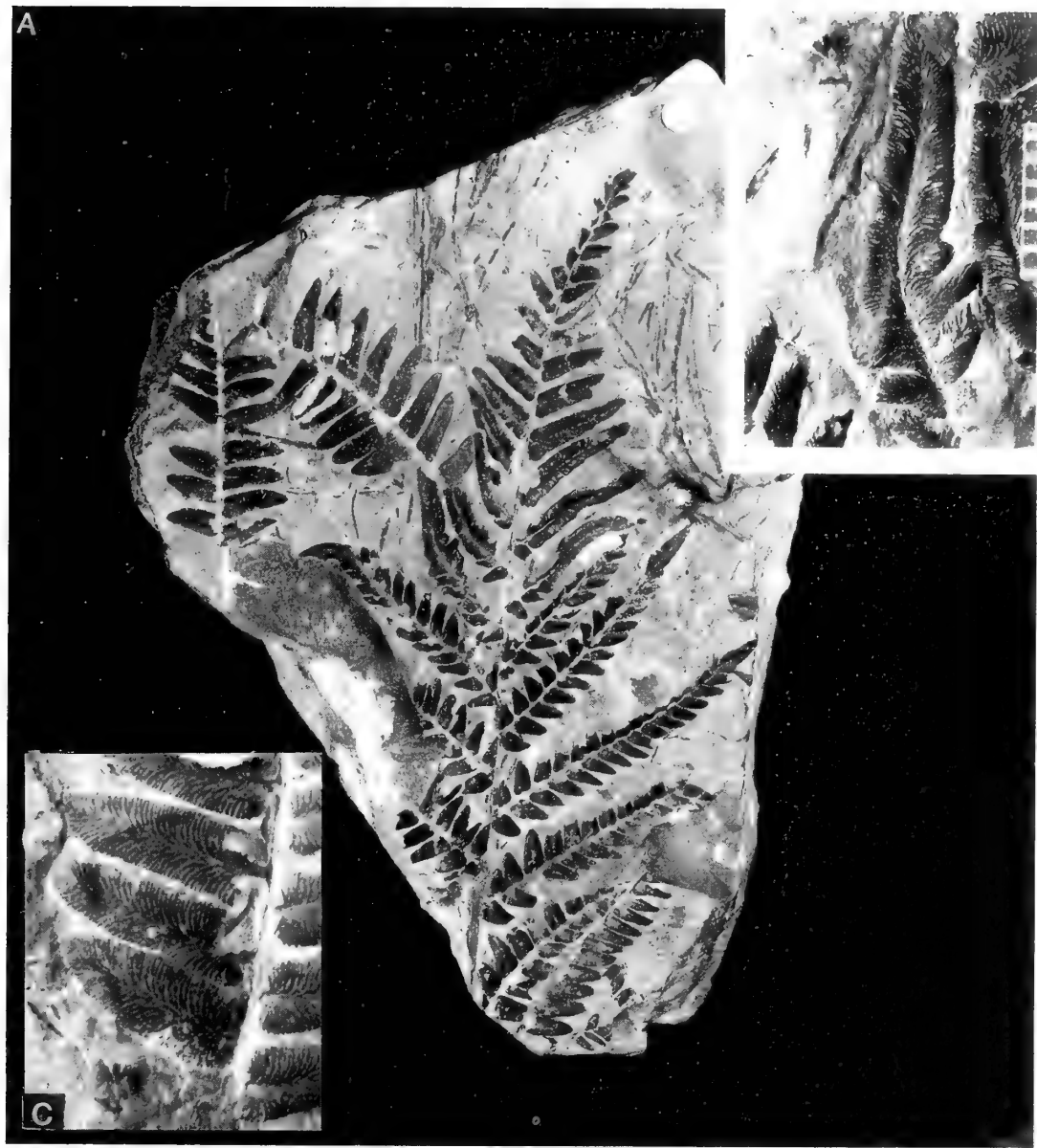
Fig. 8 *Neuralethopteris schlehanii* (Stur) Laveine. V.1301. Langsettian (Westphalian A), Oldbury, West Midlands, UK. A, whole specimen, × 1. B,C, close-ups of pinnules, × 3.
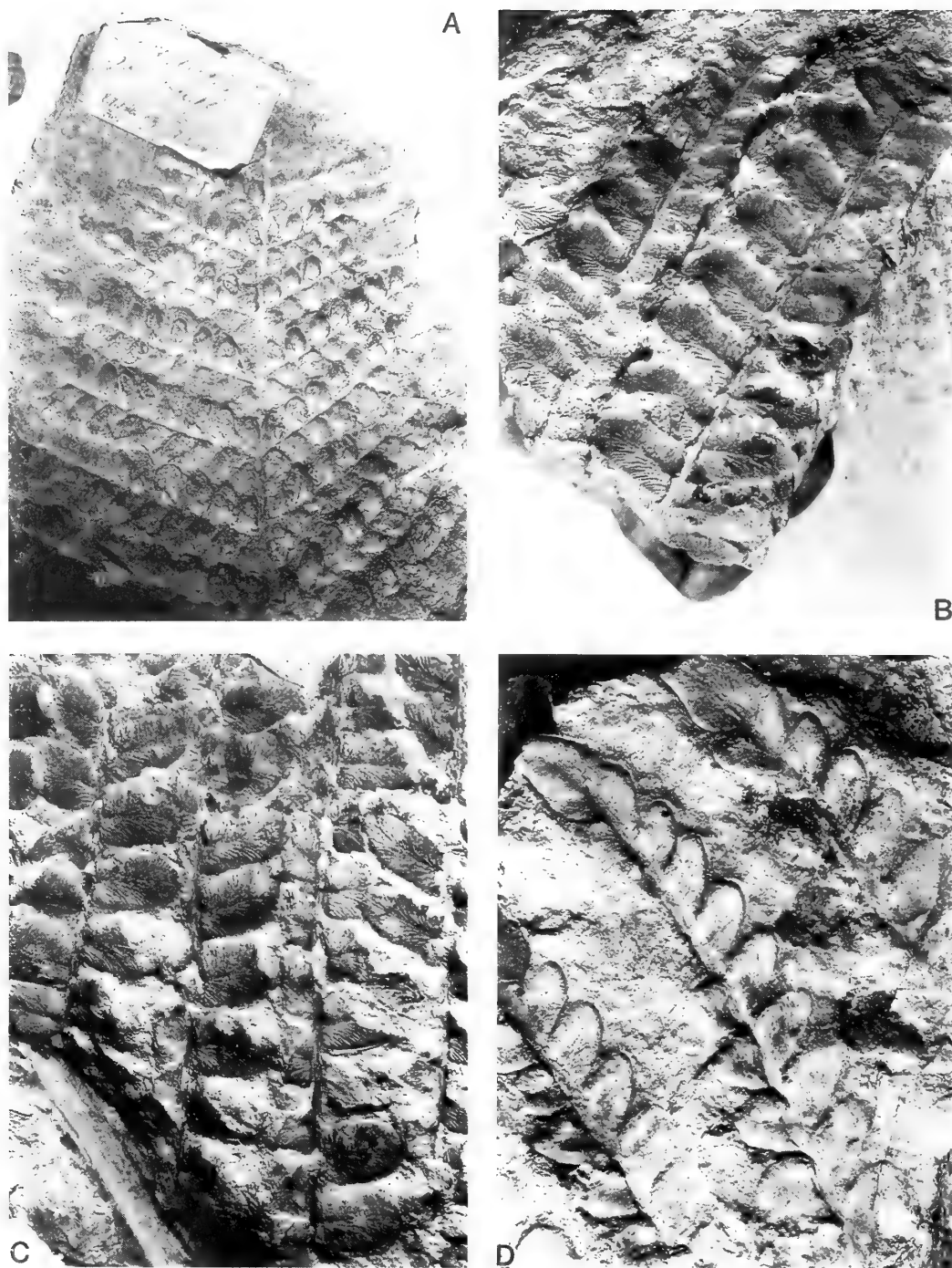
Fig. 9 *Neurocallipteris neuropteroides* (Göppert) Cleal *et al.* Richter Collection, Zwickau Museum, Germany. Lower Porphyrtuff, Planitzer Schichten (Lower Permian), Reinsdorf, Erzgebirge, Germany (type locality). A, × 1. B–D, × 1·5. Illustrations prepared from negatives provided by Professor. M. Barthel.
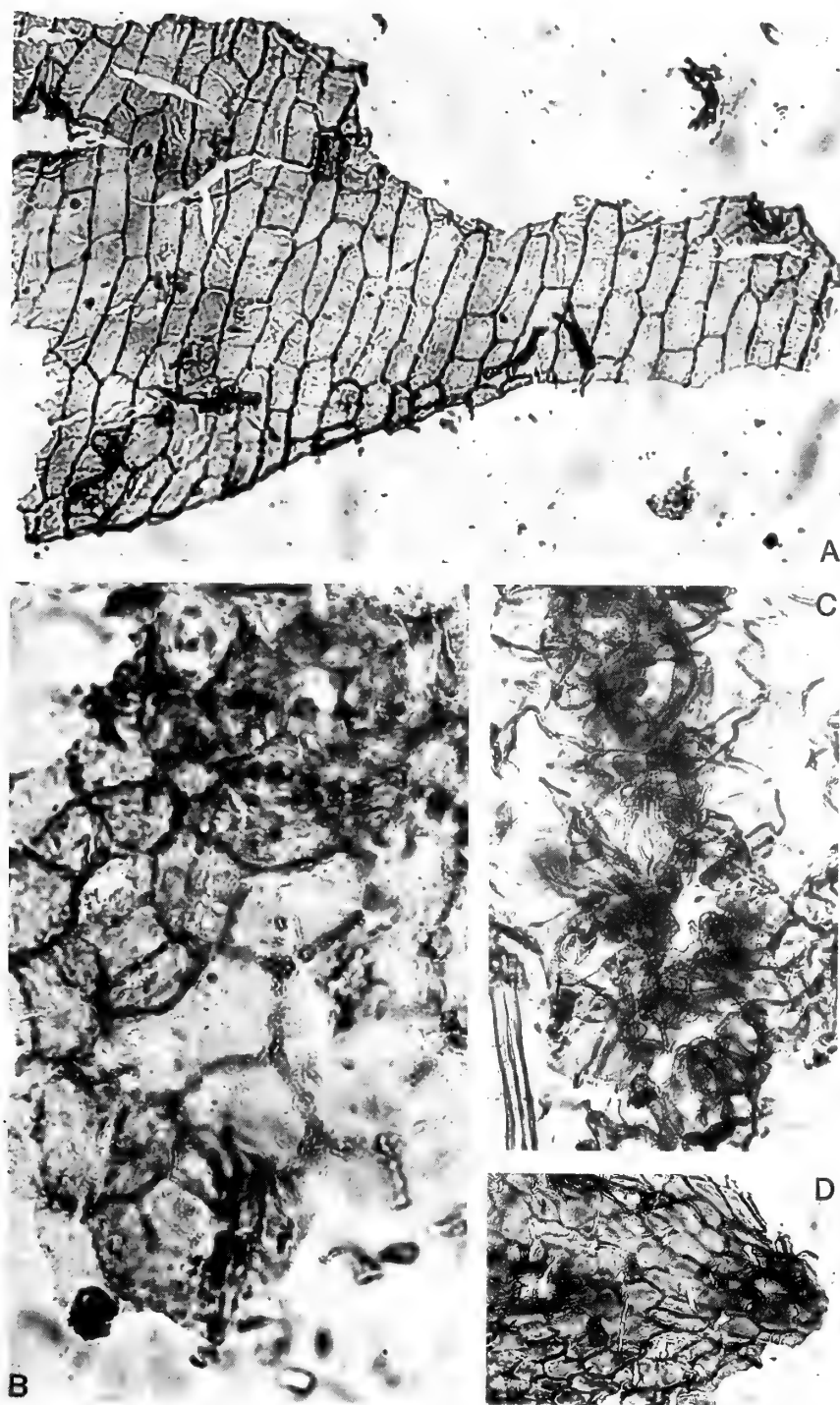
Fig. 10 *Neurocallipteris neuropteroides* (Göppert) Cleal *et al.* Slides stored in the Museum für Naturkunde, Berlin. Härtensdorfer Schichten (Lower Permian), Hedwig Shaft (Wilde Collieries), Oelsnitz, Erzgebirge, Germany. A, adaxial cuticle, Slide No. I/89, × 200. B, brachyparacytic stomata on abaxial cuticle, Slide No I/89, × 500. C, papillae surrounding stomata on abaxial cuticle, Slide No II/61, × 500. D, stomata from near the edge of an abaxial cuticle, Slide No. I/89, × 200. Illustrations prepared from negatives provided by Professor. M. Barthel.
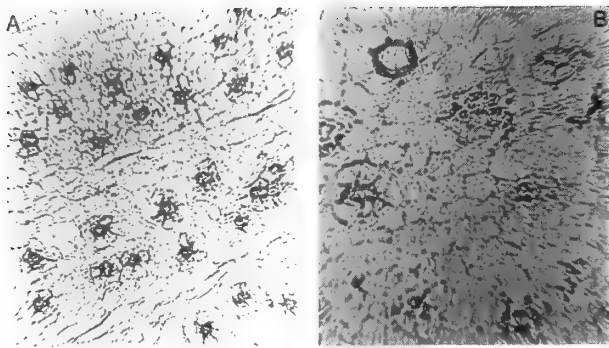
Fig. 11 *Neurodontopteris auriculata* (Brongniart) Potonié. Czech Geological Survey, Slide No. 226/1. Lower Stephanian B, Jívka Member, Odolov Formation, Kateřina Mine, Radvanice, Bohemia (Intra-Sudetic Basin). A, bands of stomata in intercostal areas, × 50. B, close-up of cyclocytic stomata, × 140. Photographs provided by Dr Z. Šimůnek.
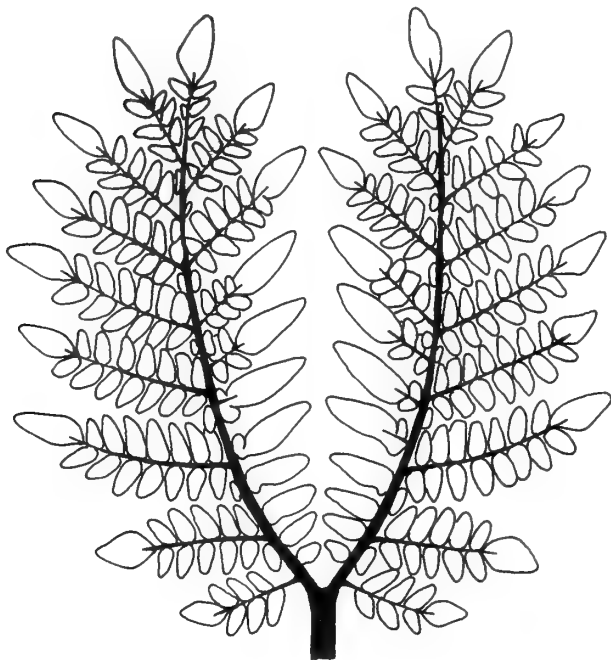
Fig. 12 Reconstruction of *Neurodontopteris* frond. Based on Langiaux (1984: fig. 233).

assigned to the form-genus *Reticulopteris* Gothan. In the lower Westphalian D, *Reticulopteris* declines in abundance, then becomes extinct to be replaced by another group of neuropterids centred on the species *N. ovata* Hoffmann. The palaeoecological background to this variation in venation is discussed in the Diversity Analysis section, later in this paper.

Distinctive characters of the pinnule cuticles are the abundant trichomes, especially on the abaxial surface, the well developed intercellular flanges on the abaxial cuticles, and the anomocytic or brachyparacytic stomata (Fig. 17A,B).

Beeler (1983) has demonstrated that *Neuropteris sensu stricto* fronds were attached to stems belonging to the form-genus *Medullosa*, providing strong support for their trigonocarpalean affinities. Evidence as to the fructifications is less

conclusive. Kidston & Jongmans (1911) have reported a sporangial organ attached to a fragment of *Neuropteris* frond, while Darrah (1937) and Zodrow & McCandlish (1980) have reported ovules in apparent attachment. However, no anatomical information has been obtained from these fructifications. Perhaps the most interesting point is that the ovules seem to be attached laterally to a pinna, replacing a lateral pinnule, whereas the laveineopterid ovules seem to have been attached to the distal end of the pinna, replacing an apical pinnule.

Form-genus *PARIPTERIS* Gothan (1941: 427)

TYPE. *P. gigantea* (Sternberg) Gothan

COMMENTS. The systematic basis of this form-genus has been thoroughly analysed by Laveine (1967). Its distinctive paripinnate frond architecture (paired apical pinnules, intercalated pinnules on the penultimate rachides) separates it from all of the other neuropteroid form-genera (Fig. 16).

There is a mesh-veined counterpart of *Paripteris*, known as *Linopteris* Presl. It would seem that it is the foliage of a distinctive group of trigonocarpalean pteridosperms, which may be referred to as the Potonieaceae (see Cleal, 1993). In addition to the distinctive frond architecture, at least one member of the family (*Linopteris obliqua* Bunbury) has been shown to have stems with a vascular system that is not as dissected as in the other trigonocarpaleans, and when preserved as a petrifaction is known as *Sutcliffia* (Stidd et al. 1975). The ovules are generally assumed to be of the type known as *Hexagonocarpus* (or *Hexapterospermum* when preserved anatomically), and are characterized by a six-fold axial symmetry (Taylor 1966), in contrast to the three-fold symmetry of other trigonocarpalean ovules. Perhaps most distinctive are the male fructifications, which consist of numerous sporangial clusters (individually known as *Potoniea*) formed into a large cone-like structure (Laveine et al. 1991). They contain trilete prepollen, in contrast to the monolete prepollen of the other trigonocarpaleans (Stidd 1978).

The morphological evidence for the distinctiveness of the Potonieaceae is also supported by its distribution (Laveine et al. 1989). The Potonieaceae originated in the Visean of China and did not appear in Laurasia until the Namurian. The rest of the Trigonocarpales, in contrast, seem to have originated in Laurasia and only a few species are found in China. Most authors still retain the Potonieaceae in the Trigonocarpales, but there is increasing evidence that it represents a totally distinct group of pteridosperms, the few similarities (e.g. detailed ovule structure) being a matter of analogy.

Form-genus *SPHENONEUROPTERIS* Shchegolev (1979: 158)

TYPE. *S. elegans* Shchegolev

COMMENTS. This refers to a group of mainly Stephanian fronds that stand apart from most other neuropteroids, in having large, relatively lax pinnules with a low vein density. Wagner (1963) and Knight (1983) put forward evidence to show that at least some of the species (*'N.' dimorpha*, *'N.' praedentata*, *'Mixoneura' wagneri*) cluster together to form a more natural group, although they did not propose a new name for the group.
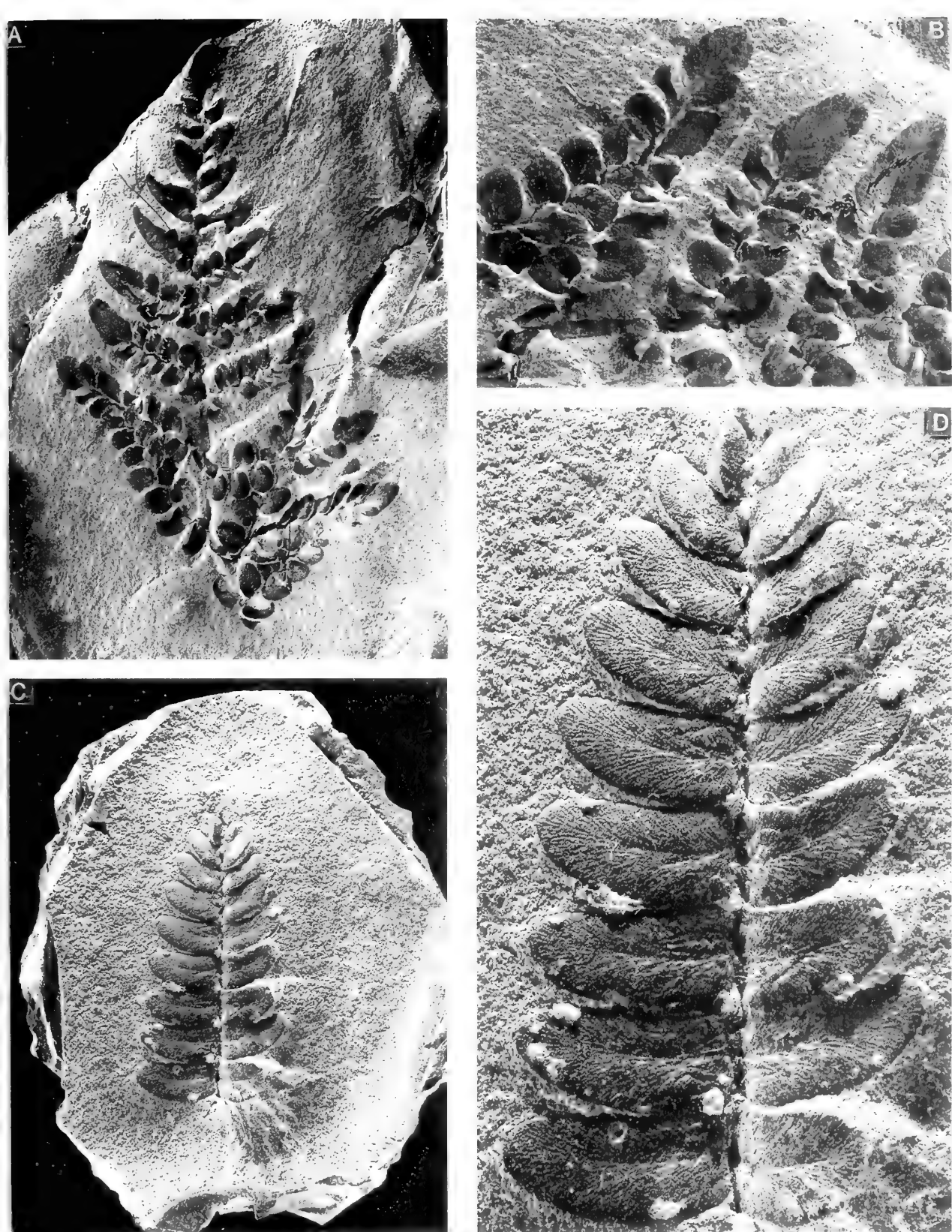
ig. 13 *Neuropteris obliqua* (Brongniart) Zeiller. V.63723. Duckmantian (Westphalian B), Rhigos, near Hirwaun, Mid-Glamorgan. UK. A, whole specimen, × 1. B, enlargement of pinnules, × 2.
Paripteris pseudogigantea (Potonié) Gothan. V.63724. Duckmantian (Westphalian B), Rhigos, near Hirwaun, Mid-Glamorgan, UK. C, whole specimen, × 1. D, enlargement of pinnules, × 3.

Fig. 14   *Neuropteris obliqua* (Brongniart) Zeiller. Duckmantian (Westphalian B), Yorkshire, UK. Photograph taken in the field of the proximal portion of a frond preserved in sandstone. Previously illustrated at lower magnification by Scott (1978: pl. 27, fig. 1). A, whole specimen, × 0·2. B, pinnate foliage from above dichotomy, × 0·5. C, pinnae attached to primary rachis below the dichotomy, × 1.

Fig. 15 *Neuropteris heterophylla* (Brongniart) Sternberg. V.1797. Duckmantian (Westphalian B), Clay Cross, Derbyshire, UK. × 0·34.
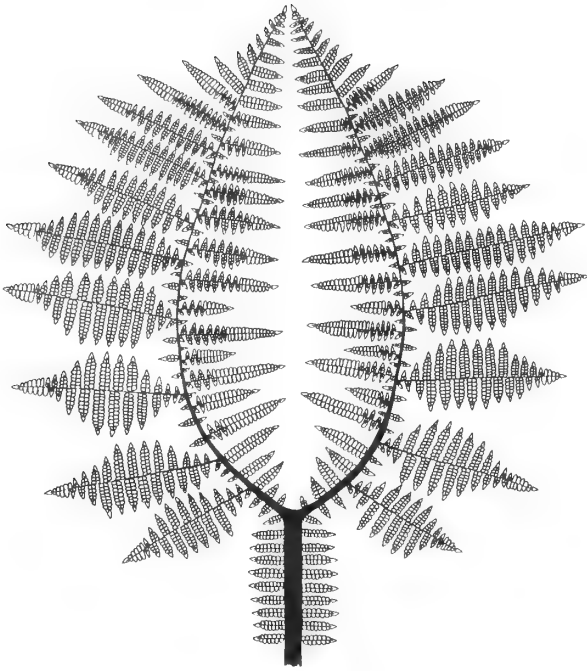
Fig. 16 Reconstruction of *Neuropteris* frond (*N. heterophylla*
(Brongniart) Sternberg). From Cleal & Shute (1991: fig. 29).

In his investigations on Stephanian plant fossils from the
Caucasus, Shchegolev (1979) described some fragments of
neuropteroid fronds, which also had relatively large, lax-
limbed pinnules and wide venation, and for which he pro-
posed the new name *Sphenoneuropteris*. We still have very
little information on the architecture of these fronds, and
nothing of the epidermal structure or fructifications. It is far
from clear, therefore, whether this is a homogeneous group
of species. However, for the time being *Sphenoneuropteris*
provides a convenient receptacle for these distinctive frond
fragments, which clearly have little to do with *Neuropteris*
sensu stricto, or probably even the Trigonocarpales in gen-
eral.

SYSTEMATICS

Form-genus *LAVEINEOPTERIS* Cleal, Shute & Zodrow

Laveineopteris guadiatensis (Wagner) Cleal & Shute,
comb nov.

*1983b *Neuropteris guadiatensis* Wagner: 95; pl. 1.

REASON FOR GENERIC ASSIGNMENT. Wagner records associ-
ated orbicular cyclopterid pinnules with the more typical
pinnate foliage of this species. Also, fragmentary cuticles
prepared by C.R. Hill (Natural History Museum) and shown
to us, display a number of laveineopterid characteristics:
adaxial cuticle shows relatively uniform cell patterns, no
anticlinal walls preserved on abaxial cuticle, and no trichomes
are preserved on either cuticle.

OCCURRENCE. S. Spain (Duc).

Laveineopteris hollandica (Stockmans) Cleal & Shute,
comb. nov.

* 1933 *Neuropteris hollandica* Stockmans: 31–34; pl. 10,
fig. 1.
v 1959 *Neuropteris rytoniana* Kidston ex Crookall:
113–114; pl. 52, figs 3–4; pl. 54, fig. 1 (vide Laveine,
1967).
.v 1959 *Neuropteris formosa* Kidston ex Crookall: 139–140;
pl. 52, figs 1–2.

REASON FOR GENERIC ASSIGNMENT. Similarity of pinnule
morphology with *L. tenuifolia*.

COMMENTS. Although its venation is not entirely typical, *N.*
formosa is taken to be a later synonym of *L. hollandica* based
on the similarity in shape of its subtriangular pinnules. Also,
the types of *N. formosa* originated from the same locality as
the types of *N. rytoniana*, which Laveine (1967) assigned to
L. hollandica.

OCCURRENCE. Pennines (Lan-Bol), Franco-Belgian Basin
(Lan-Duc), S. Limburg (Lan), NW Germany (Lan-Bol), NE
Germany (Lan-Bol).

Laveineopteris jongmansii (Crookall) Cleal & Shute,
comb. nov.

v? 1888 *Neuropteris plicata* Sternberg; Kidston: 313; pl. 1,
fig. 1.
? 1917 *Neuropteris subplicata* Kidston: 1031.
*v 1959 *Neuropteris jongmansii* Crookall: 178; pl. 51, fig. 1.
.v 1967 *Neuropteris chalardi* Laveine: 176–181; pls 35–39.

REASON FOR GENERIC ASSIGNMENT. Great similarity of pin-
nule morphology to *L. tenuifolia*.

COMMENTS. Laveine (1967) noted the close similarity
between his *N. chalardi* and the holotype of *L. jongmansii*
figured by Crookall (1959). Crookall's specimen alone was
inadequate evidence for Laveine to make a proper compari-
son. However, one of us (CJC) has examined additional
material in the collections of the British Geological Survey
and can confirm that the two species are identical.

The type and only known specimen of *N. subplicata* has
similar shaped pinnules and a dense venation. The apical
pinnule is rather small, but can be compared with the lower
end of the range of variation of *L. jongmansii* (e.g. Laveine
1967: pl. 37, fig. 2). More examples of this species are needed
but, if the synonymy can be confirmed, Kidston's species will
be the valid name.

OCCURRENCE. Pennines (Bol), Franco-Belgian Basin (Bol),
NW Germany (Bol), Lublin (Bol), NE Germany (Bol).

Laveineopteris loshii (Brongniart) Cleal, Shute &
Zodrow   Figs 4, 17C,D

* 1831 *Nevropteris Loshi* Brongniart: 242; pl. 72, fig. 1; pl.
73.
.v 1959 *Neuropteris hemingwayi* Crookall: 121–122; pl. 46,
fig. 6.
T 1967 *Neuropteris loshi* Brongniart; Laveine: pls C–D.
§ 1990 *Laveineopteris loshii* (Brongniart) Cleal, Shute &
Zodrow: 490.

REASON FOR GENERIC ASSIGNMENT. Type species.
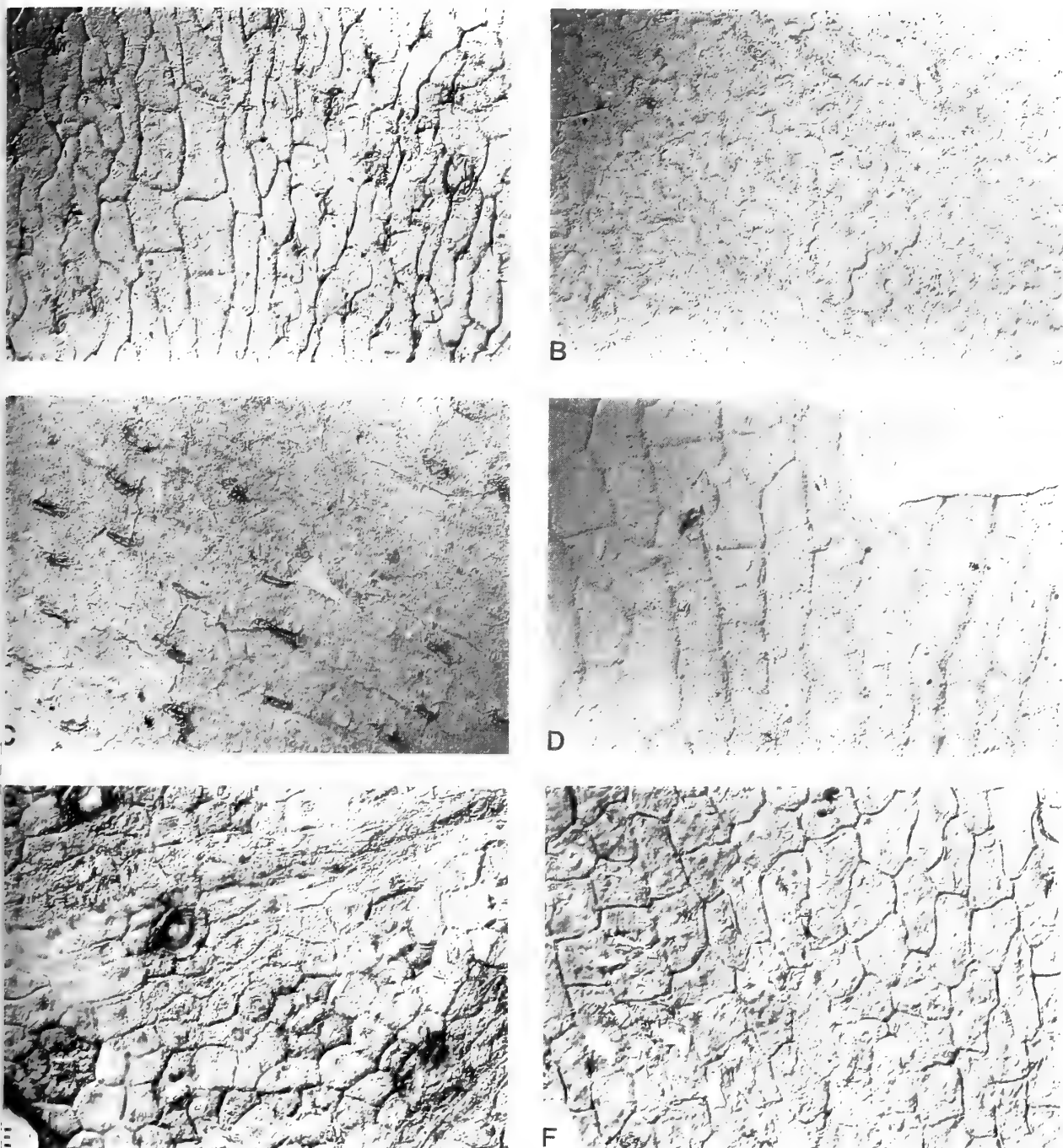
Fig. 17 Neuropteroid cuticles photographed using Normarski Interference. All × 200. A, *Neuropteris ovata* Hoffmann. Abaxial cuticle. V.62925. Basal Westphalian D, Kallenberg Seam, Itzenplitz Colliery, Saarland, Germany. B, *N. ovata*. Adaxial cuticle. V.62924. Same horizon and locality. C, *Laveineopteris loshii* (Brongniart) Cleal *et al.*. Abaxial cuticle. V.62974. Duckmantian (Westphalian B), Royosborn Colliery Borehole, North Yorkshire, UK. D, *L. loshii*. Adaxial cuticle. V.62948. Same horizon and locality. E, *Macroneuropteris macrophylla* (Brongniart) Cleal *et al.*. Abaxial cuticle. V.62295. Upper Westphalian D, Upper Bonnar Seam, Brogan's Pit, Sydney Coalfield, Cape Breton, Canada. F, *M. macrophylla*. Adaxial cuticle. V.63055. Same horizon and locality.

COMMENTS. The epidermal structure has been described by Cleal & Shute (1992) and orbicular cyclopterid pinnules have been shown attached near the base of its frond (von Roehl 1868: pl.17).

N. hemingwayi was based on a single fragment from the Parkgate Coal (upper Langsettian) of Yorkshire, from which *L. loshii* is well documented (e.g. Crookall 1959: pl.28, fig.4). It is poorly preserved, but the pinnule shape and venation seem indistinguishable from *L. loshii*.

OCCURRENCE. South-West .UK (Lan-Bol), Pennines, UK (Lan-Bol), Franco-Belgian Basin (Lan-Bol), S. Limburg (Lan), NW Germany (Lan-Bol), NE Germany (Lan-Bol), Lublin (Lan-Bol), Intra-Sudetic Basin (Duc-Bol), U. Silesia (Lan-Bol), Svoge (Duc-Bol), Donets (Lan-Duc).

Laveineopteris morinii (Bertrand ex Laveine) Cleal & Shute, comb. nov.

*   1967   *Neuropteris morinii* Bertrand ex Laveine: 227–228; pls 63–65.

REASON FOR GENERIC ASSIGNMENT. The association of orbicular cyclopterid pinnules (Laveine 1967: pl. 64 fig. 6), and general similarity of some of the pinnules to the more elongate-pinnule laveineopterids such as *L. tenuifolia* and *L. hollandica*.

COMMENTS. Laveine (1967) argued that this species belongs to the general group allied to *Neuropteris obliqua*, and would thus be retained in *Neuropteris* in its restricted sense as used here. This was based mainly on the supposed presence of forma *impar*-type pinnules. However, the best example that he illustrates to justify this opinion (Ibid. pl. 65 fig. 5) is poorly localized and there is no evidence that it was associated with more typical pinnules of this species. The other two examples (Ibid. pl. 63 figs 2–3), although in clear association with specimens showing the more typical pinnule form of this species, are isolated pinnules – one possibly a terminal, the other a lateral. Being isolated, it is far from certain that they are of the forma *impar* type from the lower part of a frond, or even that they belong to the same species.

It is true that the cyclopterid illustrated by Laveine is also only associated with the specimens of pinnate foliage. However, in view of the close similarity of the pinnules to *L. tenuifolia* (from which it can only be reliably distinguished by its denser, occasionally flexuous veins), we believe that the association with the cyclopterid reflects an original organic connection.

OCCURRENCE. Franco-Belgian Basin (Bol).

Laveineopteris nicolausiana (Gothan) Cleal & Shute, comb. nov.

*   1913   *Neuropteris nicolausiana* Gothan: 213; pl. 48; pl. 49, fig. 1.

REASON FOR GENERIC ASSIGNMENT. The similarity of the pinnule shape to *L. rarinervis* and of the venation to *L. tenuifolia*. Also, the frequent association of orbicular cyclopterids.

COMMENTS. Many authors have regarded this as indistinguishable from *L. rarinervis* (e.g. Stockmans 1933, Crookall 1959, Laveine 1967). However, it differs from that species in having (a) more linguaeform lateral pinnules, (b) lateral veins

that fork at a narrower angle and meet the pinnule margin at a more oblique angle, and (c) smaller, more ovoid apical pinnules. It is thus in some ways morphologically intermediate between typical *L. rarinervis*, and the larger-pinnuled species *L. tenuifolia*. In view of its stratigraphical occurrence at the lower end or just below the range of *L. rarinervis*, it is possible that it represents its evolutionary ancestor and a link with the larger-pinnuled *L. tenuifolia* group of species.

Bertand (1930) altered the spelling to *nikolausii*, changing it to the substantive form and reverting to the original spelling of the surname Nikolaus. However, ICBN Article 73 allows a species name to be based on an latinized personal name in an adjectival form. The original spelling is therefore retained.

OCCURRENCE. Intra-Sudetic Basin (Bol), U. Silesia (Duc-Bol), Saar-Lorraine (Duc-Bol).

Laveineopteris piesbergensis (Gothan) Cleal & Shute, comb. nov.

*   1953   *Imparipteris piesbergensis* Gothan: 57; text fig. 8; pl. 32.

REASON FOR GENERIC ASSIGNMENT. The presence of orbicular cyclopterids in the proximal part of the frond (Gothan 1953: text fig. 8), and the close similarity of the pinnules to *L. rarinervis*.

COMMENTS. Gothan distinguished this species from *L. rarinervis* by a number of characters of the orbicular cyclopterid pinnules, which are probably of doubtful taxonomic significance. However, he also mentioned that the venation of the lateral pinnules was denser and more oblique to the pinnule margin. The significance of these differences of veining pattern is not clear, and Laveine (1967) included Gothan's species in the synonymy of *L. rarinervis*. However, we have opted to maintain the distinction, at least until the German material can be more fully assessed.

OCCURRENCE. NW Germany (WeD).

Laveineopteris rarinervis (Bunbury) Cleal, Shute & Zodrow   Fig. 5

*   1847   *Neuropteris rarinervis* Bunbury: 425; pl.22.
§1990   *Laveineopteris rarinervis* (Bunbury) Cleal, Shute & Zodrow: 490.

REASON FOR GENERIC ASSIGNMENT. Epidermal structure (Cleal & Zodrow 1989) and the presence of orbicular cyclopterid pinnules near the dichotomy of a bipartite frond (Laveine 1967: pl.45, fig.3).

OCCURRENCE. South-West UK (Bol-Can), Pennines (Bol-WeD), Franco-Belgian Basin (Bol-WeD), NW Germany (Bol-WeD), NE Germany (Bol), Lublin (Duc-Bol), U. Silesia (Bol-WeD), Donets (Duc-WeD), Turkey (WeD), (?)NW Spain (WeD).

Laveineopteris tenuifolia (Sternberg) Cleal, Shute & Zodrow

T 1820   *Filicites tenuifolius* Schlotheim: 405; pl. 22, fig. 1.
*   1825   *Neuropteris tenuifolia* Schlotheim ex Sternberg: xvii
§   1990   *Laveineopteris tenuifolia* (Sternberg) Cleal, Shute & Zodrow: 490.

REASON FOR GENERIC ASSIGNMENT. Epidermal structure (Barthel 1962, Cleal 1985). Also, pinnate fragments of this species are almost invariably associated with orbicular cyclopterid pinnules.

COMMENTS. This species has been widely reported from the Iberian Peninsula. However, Cleal (1981) analysed these records and showed that they were based either on specimens of *Neuropteris resobae* Cleal (q.v.), or on unidentifiable fragments; *L. tenuifolia* would seem to be absent from this area.

OCCURRENCE. South-West UK (Lan-WeD), Pennines (Lan-Bol), Franco-Belgian Basin (Lan-WeD), S. Limburg (Lan), NW Germany (Lan-WeD), Lublin (Lan-Bol), Intra-Sudetic Basin (Duc-Bol), U. Silesia (Lan-Bol), Saar-Lorraine (Bol), Svoge (Duc-Bol), Donets (Duc-WeD).

Form-genus *MACRONEUROPTERIS* Cleal, Shute & Zodrow

Macroneuropteris britannica (Gutbier) Cleal, Shute & Zodrow

* 1835 *Odontopteris britannica* Gutbier: 68, pl. 9, figs 8–11.
§ 1990 *Macroneuropteris britannica* (Gutbier) Cleal, Shute & Zodrow: 488.

REASON FOR GENERIC ASSIGNMENT. Epidermal structure (Barthel 1962).

OCCURRENCE. Zwickau-Oelsnitz (WeD).

Macroneuropteris macrophylla (Brongniart) Cleal, Shute & Zodrow   Figs 6–7 17E–F

* 1831 *Nevropteris macrophylla* Brongniart: 235; pl. 65, fig. 1.
§ 1990 *Macroneuropteris macrophylla* (Brongniart) Cleal, Shute & Zodrow: 488.

REASON FOR GENERIC ASSIGNMENT. Type species.

COMMENTS. Cuticles have been described by Cleal & Zodrow (1989). The frond architecture is currently under review by Cleal, Laveine & Shute.

The specimens from North Caucasus illustrated by Anisimova (1979) as this species are clearly misidentified. They are isolated pinnules which resemble those of *Paripteris* (e.g. *P. pseudogigantea*), although they would seem to have originated from rather a high stratigraphical position (WeD) for that form-genus.

OCCURRENCE. South-West UK (WeD-Can)

Macroneuropteris scheuchzeri (Hoffmann) Cleal, Shute & Zodrow

* 1827 *Neuropteris scheuchzeri* Hoffmann: 157; pl. 1b, figs 1–4.
§ 1990 *Macroneuropteris scheuchzeri* (Hoffmann) Cleal, Shute & Zodrow: 488.

REASON FOR GENERIC ASSIGNMENT. Epidermal structure (Barthel 1961, Cleal & Zodrow 1989). The frond architecture is currently under review by Cleal & Laveine.

COMMENTS. Havlena (1953: pl. 5, fig. 3) figured a fragment reputedly from the Stephanian C of the Intra-Sudetic Basin as *Neuropteris cordata*. He claimed similar material also occurred in the Autunian of this region. As pointed out by Laveine (1967), however, the figured specimen is almost certainly *M. scheuchzeri*. If it does belong there and its stated provenance is correct, this is by far the highest stratigraphical occurrence of this species in Europe.

OCCURRENCE. South-West UK (Duc-Can), Pennines (Lan-Bol), Franco-Belgian Basin (Duc-WeD), S. Limburg (Duc), NW Germany (Duc-WeD), NE Germany (Duc-Bol), Lublin (Bol), Intra-Sudetic Basin (Duc-WeD, ?StC-Aut), U. Silesia (Lan-Bol), Saar-Lorraine (Bol)́, Alps (Can), Svoge (Bol), Donets (Duc-WeD), N. Caucasus (WeD), Turkey (WeD), N. Portugal (WeD), NW Spain (WeD-Can), S. Portugal (WeD).

Macroneuropteris subauriculata (Sterzel) Cleal, Shute & Zodrow

T 1855 *Neuropteris auriculata* Brongniart: Geinitz: pl. 27, figs 4–7, 9.
* 1901 *Neuropteris subauriculata* Sterzel: 100.
§ 1990 *Macroneuropteris subauriculata* (Sterzel) Cleal, Shute & Zodrow: 488.

REASON FOR GENERIC ASSIGNMENT. Epidermal structure (Barthel 1962) and possibly frond architecture (Daber 1957).

COMMENTS. This species appears to be endemic to the Zwickau-Oelsnitz Basin. The record from North Caucasus by Anisimova (1979) is based on extremely poorly preserved material and is unconvincing.

Laveine (1989: pl. 60, fig. 1) has figured a single fragment of this species from the upper Westphalian D (or possibly basal Cantabrian) of Saar-Lorraine. It bears a close similarity to the fragmentary types of *Neuropteris germeri* de Jong, from slightly older strata in Saar-Lorraine, and which we have provisionally assigned to *N. ovata*. Cuticles from this Saar-Lorraine material could help resolve their taxonomic position.

OCCURRENCE. Zwickau-Oelsnitz (WeD).

Form-genus *MARGARITOPTERIS* Gothan

Margaritopteris multivenosa (Purkyňová) Cleal & Shute, comb. nov.

* 1970 *Neuropteris multivenosa* Purkyňová: 223–224; pl. 45, fig. 1, pl. 46, fig. 1.

REASON FOR GENERIC ASSIGNMENT. The prominent midvein and the size and texture of the pinnules (see Laveine *et al.* 1977). Also the manner of lobing of the pinnules.

COMMENTS. Laveine *et al.* (1977) were clearly of the opinion that this species belongs to *Margaritopteris*, and was the precurssor of the more familiar Westphalian species, although no formal proposal of transference was made. The factors mentioned above, particularly well shown in Laveine *et al.* (1977, pl. 19, fig. 3), make' it unnecessary to postpone the proposal of transference.

OCCURRENCE. U. Silesia (Alp).

Form-genus *NEURALETHOPTERIS* Cremer ex Laveine

Neuralethopteris densifolia Josten

* 1983 *Neuralethopteris densifolia* Josten: 144; pl. 53, fig. 1; pl. 54, fig. 1.

REASON FOR GENERIC ASSIGNMENT. The alethopteroid nature of the venation.

OCCURRENCE. NW Germany (Kin-Yea).

Neuralethopteris doubravica (Purkyňová) Cleal & Shute, comb. nov.

* 1971 *Neuropteris doubravica* Purkyňová: 165–166; pls 6–9.

REASON FOR GENERIC ASSIGNMENT. The cordate base of the pinnules and the prominent midvein.

COMMENTS. The generic position of this species is far from certain. At least some of the specimens figured in the protologue, particularly those with smaller pinnules, approach *Neuropteris* in venation and pinnule shape (e.g. pl. 8, fig. 1a). As pointed out by Purkyňová, however, the larger pinnules share many characters with *Neuralethopteris*, especially *N. jongmansii*, and so we propose to transfer the species there.

OCCURRENCE. U. Silesia (Lan).

Neuralethopteris jongmansii Laveine

* 1967 *Neuralethopteris jongmansii* Laveine: 107; pls 2–4.

REASON FOR GENERIC ASSIGNMENT. The typically alethopterid nature of venation (Laveine 1967). Also, *Whittleseya* sporangial structures and *Trigonocarpus* ovules have been linked by Jongmans (1954) to foliage identified as *N. jongmansii* by Laveine (1967).

OCCURRENCE. South-West UK (Lan), Pennines (Lan), Franco-Belgian Basin (Lan), S. Limburg (Lan), NW Germany (Lan), U. Silesia (Lan).

Neuralethopteris larischii (Šusta) Laveine

* 1930 *Neuropteris Larischi* Šusta: 5, pl.1.
§ 1967 *Neuralethopteris larischi* (Šusta) Laveine: 102; pl. 1.

REASONS FOR GENERIC ASSIGNMENT. Typically alethopterid nature of venation (Laveine 1967).

OCCURRENCE. Franco-Belgian Basin (Arn-Lan), NW Germany (Arn-Lan), U. Silesia (Kin-Lan), N. Caucasus (?Kin-?Yea), Turkey (Yea), NW Spain (Lan).

Neuralethopteris neuropteroides (Šusta) Josten

* 1927 *Alethopteris neuropteroides* Šusta: 4; pl. 1, fig. 2.
§ 1983 *Neuralethopteris neuropteroides* (Šusta) Josten: 138; pl. 50, fig. 1.

REASON FOR GENERIC ASSIGNMENT. The close similarity in pinnule shape to *N. schlehanii*, and the tendency of the pinnules to be fused to the rachis at the base.

COMMENTS. This species seems to occupy a position intermediate between *Neuralethopteris* and true *Alethopteris*.

OCCURRENCE. Franco-Belgian Basin (Kin-Lan), NW Germany (Kin-Lan), U. Silesia (Yea-Lan).

Neuralethopteris rectinervis (Kidston) Laveine

*v 1888 *Neuropteris rectinervis* Kidston: 314; pl.1, figs 2–4.
T 1959 *Neuropteris Schlehani* forma *rectinervis* (Kidston) Crookall: 145–147; pl. 35, figs 6–8.
§ 1967 *Neuralethopteris rectinervis* (Kidston) Laveine: 120; pl. 9.

REASON FOR GENERIC ASSIGNMENT. typically alethopterid nature of venation (Laveine 1967).

OCCURRENCE. South-West UK (Lan), Pennines (Lan), Franco-Belgian Basin (Lan), NW Germany (Lan), U. Silesia (Lan), Donets (Lan).

Neuralethopteris schlehanii (Stur) Laveine   Fig. 8

* 1877 *Neuropteris Schlehani* Stur: 289; pl.28, figs 7–8.
. 1953 *Neuropteris schlehanioides* Stockmans & Willière: 233; pl. 31, figs 3, 7; pl. 36, fig. 2.
.? 1953 *Neuropteris loriformis* Stockmans & Willière: 234; pl. 16, fig. 2.
. 1977 *Neuropteris rectinervis* forma *obtusa* Tenčov: 59–60; pl. 20, figs 3–4.
. 1977 *Neuropteris lata* Tenčov: 60; pl. 21, figs 2–3.
. 1977 *Neuropteris longifolia* Tenčov: 61; pl. 21, figs 4–9.

REASON FOR GENERIC ASSIGNMENT. Type species.

COMMENTS. Epidermal structures have been described by Cleal & Shute (1992). Also, *Aulacotheca* sporangial structures were reported in close association with it by Laveine (1967: pl.5, fig.3).

The types of *N. schlehanioides* clearly represent fragments from high in the pinna of *N. schlehanii* and can be compared with parts of Laveine (1967: pl. 6, figs 2–3). The type of *N. loriformis* is less typical, having extremely long, slender pinnules. As pointed out by Stockmans & Willière (1953), however, it occurs in association with *N. schlehanii* and has a comparable venation pattern.

Neuropteris longifolia and *N. lata* were erected for specimens from the Svidnaya Formation of the Svoge Basin. The pinnules are rather large (up to 30 mm long), but are otherwise very similar to *N. schlehanii*, with which they are closely associated. As Laveine (1967: pl. 8) has figured specimens of *N. schlehanii* with pinnules approaching these in size, there seems little reason for separating these species.

Tenčov (1977) described the types of *N. rectinervis* forma *obtusa* as having a venation nearer to that of *N. rectinervis* than *N. schlehanii*. However, the veining is in fact quite compatible with *N. schlehanii*, being broadly arched (cf. Laveine 1967: pl. 7 fig. 1; pl. 8 fig. 4).

OCCURRENCE. South-West UK (Lan), Pennines (Lan), Franco-Belgian Basin (Pen-Lan), S. Limburg (Lan), NW Germany (Mrd-Lan), NE Germany (Kin-Lan), (?)Lublin (Kin-Yea), Intra-Sudetic Basin (Lan), U. Silesia (Alp-Lan), Svoge (Yea-Lan), Donets (Pen-Lan), N. Caucasus (?Kin-Lan), Turkey (Lan), Alps (Lan), Pyrenees (Kin), NW Spain (Lan).

Form-genus *NEUROCALLIPTERIS* Sterzel

Neurocallipteris gallica (Zeiller) Cleal & Shute, comb. nov.

* 1888a *Neuropteris gallica* Zeiller: 248; pl. 29, figs 1–3.

REASON FOR GENERIC ASSIGNMENT. Close similarity to *N. planchardii* in both pinnule shape and venation.

COMMENTS. This species is not well documented, and it is not entirely certain that it is distinct from *N. planchardii*. As pointed out by Wagner (1963), many of the differences claimed by Zeiller may be merely a function of the position of the pinnules within a frond. The most obvious difference is the presence of hairs near the midvein of *N. gallica*, but this could be influenced by taphonomic factors. There have, however, been a number of records of the species in recent years, and so it has provisionally taken to be 'good'.

OCCURRENCE. Saar-Lorraine (Bar), Massif Central (StC), NW Spain (StB), S. Spain (StC), N. Portugal (StC).

Neurocallipteris neuropteroides (Göppert) Cleal, Shute & Zodrow   Figs 9–10

* 1836 *Gleichenites neuropteroides* Göppert: 186; pls 4–5.
§ 1990 *Neurocallipteris neuropteroides* (Göppert) Cleal, Shute & Zodrow: 489.

REASON FOR GENERIC ASSIGNMENT. Type species.

COMMENTS. Epidermal structure (Barthel 1962, 1976) and frond architecture (Barthel 1976, Šetlík 1980) have been documented for this species.

OCCURRENCE. Saxony (Aut), Intra-Sudetic Basin (StB-Aut), Massif Central (StC), Pyrenees (StC), NW Spain (StC), N. Portugal (StC-Aut).

Neurocallipteris planchardii (Zeiller) Cleal, Shute & Zodrow

* 1888a *Neuropteris planchardii* Zeiller: 246; pl. 28, figs 8–9.
§ 1990 *Neurocallipteris planchardii* (Zeiller) Cleal, Shute & Zodrow: 489.

REASON FOR GENERIC ASSIGNMENT. Similarity of epidermal structures to *N. neuropteroides* (see Reichel & Barthel 1964, Barthel 1976)

OCCURRENCE. Saxony (Aut), Intra-Sudetic Basin (Aut), N. Caucasus (StC), Alps (?Can), Massif Central (StB-Aut), Pyrenees (StC), NW Spain (WeD-StB), N. Portugal (StC-Aut).

Form-genus *NEURODONTOPTERIS* Potonié

Neurodontopteris auriculata (Brongniart) Potonié   Figs 11–12

  1830 *Nevropteris auriculata* Brongniart: pl. 36.
  1831 *Nevropteris auriculata* Brongniart: 236.
  1831 *Nevropteris dufrenoyi* Brongniart: 246.
  1893 *Neurodontopteris auriculata* (Brongniart) Potonié: 124.

.(?)1937 *Neuropteris densinervosa* (Grigoriev) Zalessky: 183; fig. 31.

REASON FOR GENERIC ASSIGNMENT. Type species.

COMMENTS. There have been no descriptions of cuticles under this species name. However, Z. Šimunek (pers. comm. 1992) has shown that cuticles described by Barthel (1976) as *Neuropteris cordata* in fact belong to *Neurodontopteris auriculata*. In contrast to typical *N. cordata* from the Massif Central, the specimens which yielded the cuticles have smaller pinnules (<60 mm long) with a rounder apex, and a denser venation (30 veins per cm on the pinnule margin). Šimůnek has prepared very similar cuticles from specimens of *N. auriculata* from the Intra-Sudetic Basin, examples of which are shown in Fig. 11.

The inclusion of *N. densinervosa* here must be regarded as tentative, since only two specimens have been illustrated in the literature and one of those (the holotype) only as a drawing. However, the large pinnules and high stratigraphical position (Gzhelian) of the specimens would seem compatible with *N. auriculata*.

OCCURRENCE. Saar-Lorraine (Aut), Saxony (Aut), Intra-Sudetic Basin (StB-Aut), NW Spain (StB), S. Spain (StC-Aut).

Form-genus *NEUROPTERIS* (Brongniart) Sternberg

Neuropteris antecedens Stur

* 1875 *Neuropteris antecedens* Stur: 53; pl.15, figs 1–6.
. 1953 *Neuropteris mathieui* Stockmans & Willière: 227.
. 1955 *Neuropteris condrusiana* Stockmans & Willière: 12; pl. 6, figs 1–7, 9–15; pl. 9, figs 1–8.
. 1955 *Neuropteris papilioniformis* Stockmans & Willière: 13; pl. 2, fig. 3.
. 1955 *Neuropteris pseudozamites* Stockmans & Willière: 13, pl. 2, fig. 1.

REASON FOR GENERIC ASSIGNMENT. The tendency of the pinnules to be broadly attached to the rachis and on the venation sometimes being flexuous (Crookall 1959).

COMMENTS. The type of *N. mathieui* was found associated with typical specimens of *N. antecedens*, and it is difficult to see why it is not merely the small-pinnuled form of that species.

The types of *N. condrusiana*, *N. papilioniformis* and *N. pseudozamites* all originated from the same horizon and locality, and were associated with a specimen which Stockmans & Willière (1955) identified as their *N. mathieui*. All of this material clearly belongs to a single species, and bears quite a striking similarity to the types of *N. antecedens*; it in fact represents one of the best documentations in the literature of the morphological variability of that species.

OCCURRENCE. South-West UK (Arn), Pennines (Asb-Arn), Franco-Belgian Basin (Pnd-Arn), U. Silesia (Asb-Arn), Svoge (?Arn).

Neuropteris bohdanowiczii (Zalessky) Gothan

* 1907 *Sphenopteris bohdanowiczi* Zalessky: 33, 65; pl. 2, fig. 2.

§ 1913 *Neuropteris bohdanowiczi* (Zalessky) Gothan: 210;
        pl. 44, fig. 4; pl. 53, fig. 1.

REASON FOR GENERIC ASSIGNMENT. The relatively weakly developed midvein, the slightly flexuous lateral veins, and the tendency of the pinnules to be fused to the rachis.

COMMENTS. This is a relatively poorly known species, the best documented records being by Gothan (1913) and Kotasowa (1968). Zalessky (1907) suggested that it should be placed in a new subgenus, *Sphenopteris* subg. *Neurosphenopteris*. However, it is doubtful if the latter is validly published according to the ICBN (Danzé 1956).

OCCURRENCE. U. Silesia (Alp).

Neuropteris ervedosensis (Teixeira) Wagner

* 1942 *Mixoneura ervedosensis* Teixeira: 8; pl. 1.
§ 1963 *Neuropteris ervedosensis* (Teixeira) Wagner: 27.

REASON FOR GENERIC ASSIGNMENT. The apparent occurence of enlarged, 'forma *impar*'-like pinnules in the lower part of the frond. Also, the veining, although rather less dense, has some resemblance to that of *N. ovata* and *N. flexuosa*.

COMMENTS. Opinion is divided as to the affinities of this species. De Jong (1974) regards it as being closely related to *N. ovata*, while Wagner & Sousa (1983) state that there is probably no relation with this species or *N. flexuosa*. As stated above, its affinities seem to lean towards *Neuropteris*, particularly as it probably has enlarged pinnules low in the frond, but this must be taken as provisional, at least until better information on the frond architecture becomes available.

OCCURRENCE. N. Portugal (WeD).

Neuropteris flexuosa Sternberg

T 1823 *Osmunda gigantea*, var. β Sternberg: pl.32, fig.2.
* 1825 *Neuropteris flexuosa* Sternberg: xvi.
T 1959 *Neuropteris ovata* Hoffmann, forma *flexuosa* (Sternberg) Crookall: text-fig. 52.

REASON FOR GENERIC ASSIGNMENT. Epidermal structures (Cleal & Zodrow 1989) and close similarity of pinnule form to *N. ovata*.

COMMENTS. The European records of this species, other than those in Britain, are misidentifications of species such as *Laveineopteris tenuifolia* (e.g. Novik 1952, 1954) and *L. jongmansii* (e.g. Corsin 1932).

OCCURRENCE. South-West UK (WeD-Can), S Portugal (WeD).

Neuropteris ghayei Stockmans & Willière

T 1933 *Neuropteris grangeri* Brongniart; Stockmans: pl.12, fig.3.
* 1954 *Neuropteris ghayei* Stockmans & Willière *in* Pastiels & Willière: 59.

REASON FOR GENERIC ASSIGNMENT. Underlying similarity in pinnule form with *N. heterophylla* and *N. obliqua*. Also, on the presence of large '*impar*'-type pinnules (Laveine 1967: pl.49, fig.5), similar to those found in the lower part of the *N. obliqua* frond.

OCCURRENCE. Franco-Belgian Basin (Lan), NW Germany (Lan)

Neuropteris heterophylla (Brongniart) Sternberg   Figs 15–16

* 1822 *Filicites (Nevropteris) heterophyllus* Brongniart: 239; pl. 2, fig. 6.
§ 1825 *Neuropteris heterophylla* (Brongniart) Sternberg: xvi.
T 1831 *Nevropteris (sic) heterophylla* Brongniart: pl. 71 (neotype – vide Laveine, 1967).
T 1967 *Neuropteris heterophylla* Brongniart (*sic*); Laveine: pl. A.

REASON FOR GENERIC ASSIGNMENT. Type species.

COMMENTS. Both epidermal structures and frond architecture have been documented by Cleal & Shute (1991a). Specimens of this species have sometimes been recorded as *Neuropteris grangeri* Brongniart (see comments by Laveine 1967).
    The specimens from the Donets that have been illustrated in the literature as *N. heterophylla* appear to be misidentified specimens of *Laveineopteris loshii* (Novik 1952: pl. 61, figs 1–4; 1954: pl. 20, figs 5–6). However, Fissunenko and Laveine (1984) claim that true *N. heterophylla* occurs here and, in view of Laveine's familiarity with the type specimens, the record has been accepted.

OCCURRENCE. Pennines (Duc), Franco-Belgian Basin (Lan-Bol), NW Germany (Lan-Bol), U. Silesia (Lan-Duc), Donets (Yea-WeD).

Neuropteris obliqua (Brongniart) Zeiller   Figs 13A–B, 14

T 1833 *Pecopteris obliqua* Brongniart: pl. 96, figs 1–4.
* 1834 *Pecopteris obliqua* Brongniart: 320–321.
§ 1888b *Neuropteris obliqua* (Brongniart) Zeiller: 284–289.
   1953a *Neuropteris marginenervis* Jongmans: 15; pl. 5, figs 29–30; pl. 6, figs 31–32 (vide Laveine, 1967).
.v 1959 *Neuropteris lanarkiana* Kidston ex Crookall: 174; pl. 50, figs 1–2.
T 1967 *Neuropteris obliqua* (Brongniart) Zeiller; Laveine: pl. E, figs 1–2.

REASON FOR GENERIC ASSIGNMENT. Epidermal structures (Cleal & Shute 1992) and frond architecture (Fig. 13; Gothan 1953: fig. 7; Scott 1978: pl. 27, fig. 1).

COMMENTS. The frond architecture of this species has still to be fully documented, but the available evidence suggests that it was essentially similar to that of *N. heterophylla*, except that the pinnules at the base of the frond were rather larger (the so-called 'forma *impar*'-type – e.g. Crookall (1959: pl.47, fig.4).
    Crookall (1959) distinguished *N. lanarkiana* from *N. obliqua* by its more slender, triangular and widely-spaced pinnules, and less dense and straighter veins. However, such pinnules are not atypical in the *N. obliqua* fronds, and can be compared with a specimen figured by Laveine (1967: pl. 50, fig. 1a).
    Stockmans & Willière (1965: pl. 3, fig. 8; pl. 5, figs 1–2) document specimens from NW Spain as this species, and Laveine (1967) has agreed with the identity of at least some of

them. However, the specimens are very fragmentary and, on their own, are inadequate for identification. There are no better documented specimens of this species from the Iberian Peninsula (the records by Wagner & Bowman 1983 and Alvarez-Vázquez *in* Wagner 1990 are unillustrated).

OCCURRENCE. South-West UK (Lan-Duc), Pennines (Lan-Bol), Franco-Belgian Basin (Mrd-Bol), S. Limburg (Lan-Duc), NW Germany (Mrd-Bol), NE Germany (Yea-Bol), Lublin (Lan-Bol), U. Silesia (Yea-Bol), Intra-Sudetic Basin (Lan), Svoge (Lan), Donets (Yea-Bol), N. Caucasus (?Kin-Lan), Turkey (Yea-Duc), Alps (Lan-Alps), S. Spain (Duc).

Neuropteris ovata Hoffmann   Fig. 17A–B

* 1826 *Neuropteris ovata* Hoffmann: 266.
T 1827 *Neuropteris ovata* Hoffmann: pl. 1b, fig. 6 (vide Satzwedel, 1969).
. 1888a *Nevropteris stipulata* Zeiller: 255; pl. 29 fig. 5 (tentatively suggested by Wagner & Alvarez-Vázquez, 1991).
.p 1960 *Neuropteris valdensis* (Heer) Jongmans: 57; pl. 18, fig. 117.
T 1969 *Imparipteris ovata* (Hoffmann) Gothan; Saltzwedel: pl. 24 figs 1–2.
.v 1973 *Mixoneura polyneura* Doubinger & Germer: 50–51; pl. 1, fig. 2.
.? 1974 *Neuropteris germeri* de Jong: 58; pls 21–22.
.v 1975a *Neuropteris pilosa* Doubinger & Germer: 18; pl. 7, fig. 1.

REASON FOR GENERIC ASSIGNMENT. Epidermal structures (Barthel 1962, Cleal 1985, Cleal & Zodrow 1989) and frond architecture (Zodrow & Cleal 1988).

COMMENTS. Cleal & Zodrow (1990) recognize varieties of this species, based partly on differences in epidermal structure. Also, Wagner (1963) assigns most of the Stephanian examples of the species to a separate variety (var. *grandeuryi* Wagner), based on the lateral veins being denser and less oblique to the pinnule margin. While recognizing that these varieties almost certainly have some biological validity, they will not be separated in this analysis.

The identity of upper Stephanian C specimens from north Portugal, described by Wagner & Sousa (1983) as *Neuropteris ovata* var. *pseudovata* Gothan & Sze, centers on one of the most contentious issues concerning the taxonomy of this species, viz. the difference between it and *Neurocallipteris neuropteroides*. There have been many analyses of this problem, the most detailed being by Zalessky (1909), Barthel (1976), Šetlík (1980) and Wagner & Sousa (1983). Šetlík and Wagner & Sousa have shown there are certain very subtle differences in pinnule form, but without the evidence of cuticles it is far from certain that they would be regarded as sufficient justification for separating them as species, let alone in different form-genera. It would seem that two quite separate groups of trigonocarpaleans have developed analogously similar pinnule morphologies, perhaps in response to similar environmental pressures. Consequently, identifying specimens with this type of pinnule in the upper Stephanian, if epidermal characters are unknown, is very difficult, if not impossible. Wagner & Sousa's Portugese specimens have some of the characters (somewhat subtriangular pinnules, veins slightly oblique to pinnule margin) that tend to be commoner in *N. neuropteroides* than *N. ovata*. We have

therefore provisionally transferred their specimens to *N. neuropteroides*. However, we recognize that this needs to be confirmed by epidermal evidence or, if this is impractical, by larger specimens showing the form of the intercalated pinnules (cf. Šetlík 1980).

M. polyneura and *N. pilosa* were separated from *N. ovata* on minor characters of venation and surface detail, and their distinction cannot be maintained (Cleal 1985). *N. germeri*, which was described mainly on just two specimens, has a veining pattern and pinnule shape compatible with the larger forms of *N. ovata*, especially those of the var. *sarana* as described by Cleal & Zodrow (1989). The veining density is a little lower than is typical, but can probably be accommodated within the lower end of the range of variation. As the types of *N. germeri* are associated with more typical fragments of *N. ovata* var. *sarana* (Bertrand) Cleal & Zodrow, there seems little reason for distinguishing them taxonomically.

The type of *N. stipulata* is strikingly similar to *N. ovata* in pinnule shape, being relatively squat, having a basiscopic auricle and a short midvein. If Zeiller's drawing of the type of *N. stipulata* is accurate, the vein density is *c*.40 veins per cm, which is compatible with the form of *N. ovata*, normally found in the Stephanian, and known as var. *grandeuryi* Wagner.

OCCURRENCE. South-West UK (WeD-Can), Pennines (WeD), Franco-Belgian Basin, (WeD), NW Germany (WeD), U. Silesia (WeD), Saar-Lorraine (WeD), Donets (?Bol-?Bar), N. Caucasus (WeD, StB), Turkey (WeD), Alps (WeD-StC), Massif Central (Bar-StB, ?StC), NW Spain (WeD-StB), S. Spain (StC).

Neuropteris parvifolia Stockmans

* 1933 *Neuropteris parvifolia* Stockmans: 28–29, pl. 8, figs 1–5.

REASON FOR GENERIC ASSIGNMENT. Similarity of pinnule morphology and underlying venation pattern to *N. obliqua* (see Laveine 1967).

OCCURRENCE. Franco-Belgian Basin (Duc-Bol), NW Germany (Duc-Bol), NE Germany (Duc-Bol), Lublin (Duc-Bol), Alps (Bol).

Neuropteris plicata Sternberg

* 1833 *Neuropteris plicata* Sternberg: 70; pl. 19, figs 1,3.

REASON FOR GENERIC ASSIGNMENT. Close similarity of the pinnules to *N. ovata*.

COMMENTS. This is so similar to *N. ovata* that it is far from certain that it is a distinct species. Although Šetlík (1921) attempted an analysis of the morphological variation of the pinnules, the results were equivocal on this point. If they are the same species, then Sternberg's species would take priority. In view of the important palaeobotanical and biostratigraphical role played by *N. ovata*, a more thorough analysis of *N. plicata* should be undertaken before any nomenclatural changes are proposed.

OCCURRENCE. Intra-Sudetic Basin (WeD).

Neuropteris praeovata (Němejc) Cleal & Shute, comb. nov.

*   1949   *Mixoneura praeovata* Němejc: 17–18; text fig. 2; pl. 4, figs 1–7.

REASON FOR GENERIC ASSIGNMENT. Similarity of pinnule shape and venation to *N. ovata*.

COMMENTS. As pointed out by Němejc, this clearly belongs to the group of neuropterids allied to *N. ovata*, from which it can be reliably distinguished only by the more prominent midvein. Also, it is the only known member of this group of species to occur below the Westphalian D.

OCCURRENCE. Intra-Sudetic Basin (Bol).

Neuropteris resobae Cleal

*   1981   *Neuropteris resobae* Cleal: 79, pls 1–2.

REASON FOR GENERIC ASSIGNMENT. Dense venation with relatively weak midvein. Pinnule limb often partly fused to rachis, and with basiscopic auricle.

COMMENTS. Little is known of the frond architecture, other than that the ultimate pinnae are terminated by a single apical pinnule, and nothing of the epidermal structures. Its retention in this form-genus is thus based entirely on pinnule morphology and venation, which clearly cannot be conclusive. The only other (albeit negative) piece of evidence is that, despite the size of the collection on which the species was described, not a single cyclopterid pinnule was found in association.

OCCURRENCE. NW Spain (Duc-WeD).

Neuropteris schaeferi Doubinger & Germer

*   1975a *Neuropteris schaeferi* Doubinger & Germer: 10–11; pl. 4, fig. 1.

REASON FOR GENERIC ASSIGNMENT. Similarity of epidermal structure to *N. ovata* (see Saltzwedel 1968).

COMMENTS. This species is not really adequately documented, as only one small specimen has been described in the literature. However, in view of the epidermal evidence presented by Saltzwedel (1968), it has been included in the present analysis.

OCCURRENCE. Saar-Lorraine (StB).

Neuropteris semireticulata Josten

*   1962   *Neuropteris semireticulata* Josten: 39–40; pl.3, figs 2–5.

REASON FOR GENERIC ASSIGNMENT. Similarity of pinnule morphology and underlying venation pattern to *N. obliqua* (see Josten 1962).

OCCURRENCE. South-West UK (Duc-Bol), Pennines (Duc), Franco-Belgian Basin (Duc-Bol), NW Germany (Duc-Bol), Lublin (Bol).

Neuropteris willierei Laveine

*   1967   *Neuropteris willierei* Laveine: 224–227; pl.62.

REASON FOR GENERIC ASSIGNMENT. It is almost indistinguishable from *N. parvifolia*, differing only in having smaller, more broadly attached pinnules, and occurring stratigraphically lower (Laveine 1967).

OCCURRENCE. Franco-Belgian Basin (Lan-Duc), NW Germany (Lan-Duc).

Form-genus *PARIPTERIS* Gothan

Paripteris gigantea (Sternberg) Gothan

*   1821   *Osmunda gigantea* Sternberg: 33; pl.22.
§   1941   *Paripteris gigantea* (Sternberg) Gothan: 427.
T   1953   *Neuropteris gigantea* Sternberg; Havlena: pl. 4; pl. 5, fig. 2.
.v   1959   *Neuropteris maltbyensis* Crookall: 164; pl. 33, figs 7–8.
?   1965   *Paripteris veeni* Stockmans & Willière: pl. 2, figs 4–7 (vide Wagner & Bowman 1983).

REASON FOR GENERIC ASSIGNMENT. Type species.

OCCURRENCE. South-West UK (Lan-Duc), Pennines (Lan-Duc), Franco-Belgian Basin, (Mrd-Duc), NW Germany (Mrd-Bol), NE Germany (Kin-Lan), Lublin (Kin-Duc), Intra-Sudetic Basin (Lan-Bol), U. Silesia (Mrd-Bol), Svoge (Yea-Lan), Donets (Kin-Duc), N. Caucasus (?Kin-Lan), Turkey (Lan), Alps (Lan), Pyrenees (Kin), NW Spain (Mrd, Lan), S. Spain (Lan).

Paripteris linguaefolia (Bertrand) Laveine

*   1930   *Neuropteris linguaefolia* Bertrand: 31–32; pl. 15.
§   1967   *Paripteris linguaefolia* (Bertrand) Laveine: 266–267; pls 77–78.

REASON FOR GENERIC ASSIGNMENT. Frond architecture.

OCCURRENCE. Franco-Belgian Basin (Duc-Bol), NW Germany, (Bol), Lublin (Duc-Bol), Intra-Sudetic Basin (Duc-Bol), Saar-Lorraine (Duc-Bol), Donets (Duc-WeD), Turkey (Duc), Alps (Duc-Bol), NW Spain (Duc), S. Spain (Duc).

Paripteris linguaenova (Bertrand) Cleal & Shute, comb. nov.

*   1930   *Neuropteris linguaenova* Bertrand: 29; pls 13-14.

REASON FOR GENERIC ASSIGNMENT. Similarity of pinnule shape and venation to *P. linguaefolia*.

COMMENTS. Laveine (1967) assigned the types of this species to *P. pseudogigantea*. However, they are significantly larger (many are longer than 4 cm), have a thinner midvein, and lateral veins that diverge from the midvein at a narrower angle. More problematic is its distinction from *P. linguaefolia*. Bertrand (1930) separated them because *P. linguaefolia* has virtually no midvein, and 'la disposition et l'aspect des nervures sont très différents. . .'. As the types of *P. linguaenova* occur within the stratigraphical range of *P. linguaefolia*, these differences really need to be re-examined more critically. For the time being, however, the separation has been retained.

OCCURRENCE. Saar-Lorraine (Bol).

Paripteris pseudogigantea (Potonié) Gothan Fig. 13C–D

* 1897 *Neuropteris pseudogigantea* Potonié: 113; text fig.102.

. 1941 *Neuropteris scheuchzeri* forma *minor* Novik: 457; pl. 22, fig. 2.

§ 1953 *Paripteris pseudogigantea* (Potonié) Gothan: 63–64; pl. 37, figs 1–4.

REASON FOR GENERIC ASSIGNMENT. Frond architecture (Laveine 1967: pls 73–76).

OCCURRENCE. South-West UK (Duc-Bol), Pennines (Duc-Bol), Franco-Belgian Basin (Duc-Bol), NW Germany (Duc-Bol), NE Germany (Duc-Bol), Lublin (Duc-Bol), Saar-Lorraine (Duc-Bol), Donets (Duc-Bol), NW Spain (Duc).

Paripteris schuetzei (Potonié) Daber

* 1903 *Neuropteris schützei* Potonié: 399.

T 1912 *Neuropteris schützei* Potonié: 122; fig. 84.

§ 1963b *Paripteris schützei* (Potonié) Daber: 1212, fig. 2.

REASON FOR GENERIC ASSIGNMENT. Frond architecture and general aspect of pinnules.

OCCURRENCE. S. Limburg (Lan), U. Silesia (Duc).

Form-genus *SPHENONEUROPTERIS* Shchegolev

Sphenoneuropteris brongniartii Shchegolev

* 1979 *Sphenoneuropteris brongniartii* Shchegolev: 159; pl. 53, fig. 2.

REASON FOR GENERIC ASSIGNMENT. General similarity in pinnule morphology and venation with type species.

COMMENTS. The distinction between this and *S. elegans* is far from clear, and there must be a strong likelihood that they are synonyms.

OCCURRENCE. N. Caucasus (StC).

Sphenoneuropteris dimorpha (Lesquereux) Cleal & Shute, comb. nov.

T 1879 *Pseudopecopteris dimorpha* Lesquereux: pl. 35, figs 1–6.

* 1880 *Pseudopecopteris dimorpha* Lesquereux: 201.

1978 *Neuropteris dimorpha* (Lesquereux) Boersma: 59; pl. 8, fig. 3, pl. 12, figs 1–6.

REASON FOR GENERIC ASSIGNMENT. Mainly the venation (widely forking veins, oblique to pinnule margin, producing low vein density), and the large, lax-limbed pinnules.

COMMENTS. Little is known of the frond architecture and nothing of the epidermal structure of this species. However, the pinnules show a remarkable similarity, especially in their venation (e.g. Doubinger & Germer 1975b, pl. 4), to the types of *Sphenoneuropteris*.

This species is often thought to have characteristically deeply-lobed pinnules (e.g. Wagner 1958). However, Boersma (1978) showed that this was at least partially a consequence of the thin limb of the pinnules, which rarely lay flat in the matrix, and would undulate in and out of the plane along which the fossil was split. It is unlikely that this can explain all specimens with undulate margins, but the remnant examples may simply be from the distal regions of pinnae, where pinnules are in transition to ultimate pinnae.

This species was initially assigned to *Pseudopecopteris* Lesquereux, 1880. However, this form-genus was not typified and included within it was a variety of disperate types of frond; it is thus a *nomen dubium*, and cannot be used as an alternative name for *Sphenoneuropteris*.

OCCURRENCE. Saar-Lorraine (Bol-StB).

Sphenoneuropteris elegans Shchegolev

* 1979 *Sphenoneuropteris elegans* Shchegolev: 158; pl. 54, figs 1,2.

REASON FOR GENERIC ASSIGNMENT. Type species.

OCCURRENCE. N. Caucasus (StC).

Sphenoneuropteris nemejciana (Purkyňová) Cleal & Shute, comb. nov.

* 1971 *Neuropteris nemejciana* Purkyňová: 168; pls 10–11.

. 1971 *Neuropteris venceslai* Purkyňová: 171; pl. 12.

REASON FOR GENERIC ASSIGNMENT. Similarity of pinnule form and venation to *S. dimorpha*.

COMMENTS. Purkyňová's specimens occur stratigraphically lower than any of the other species included in *Sphenoneuropteris*. However, it has many of the characteristic gross morphological features of that form-genus, including large pinnules (30–35 mm long) with a lax limb and somewhat undulate margin, and a low vein density (16 veins per cm on pinnule margin).

The type and only known specimen of *N. venceslai* originated from the same locality and horizon as the types of *S. nemejciana*. It has similarly large, relatively thin-limbed pinnules, thin midvein, and low vein density; compare for instance the specimen figured by Purkyňová on her pl. 11, fig. 2. The pinnules have a more acute apex, and are marginally larger, but not execssively so; the largest recorded pinnule of *S. nemejciana* is 5.5 cm long, as opposed to 7.5 cm in *N. venceslai*. All in all, there seems little reason to regard these as separate species.

OCCURRENCE. U. Silesia (Lan).

Sphenoneuropteris praedentata (Gothan) Cleal & Shute, comb. nov.

* 1909 *Neuropteris praedentata* Gothan: figs 1,2.

REASON FOR GENERIC ASSIGNMENT. Based mainly on venation (widely forking veins, oblique to pinnule margin, producing low vein density), and the relatively large, subtriangular pinnules.

COMMENTS. The general aspect of the pinnules, particularly the venation, seems to exclude this from *Neuropteris* as it is interpreted in this work. The venation seems to fit in far better with that given in the diagnosis of *Sphenoneuropteris* given by Shchegolev (1979). It is recognized that this is far from a satisfactory basis for recognizing 'natural' form-genera. However, until cuticle and frond architecture data become available, Shchegolev's form-genus provides a convenient repository for this species.

The only large specimens of this species to have been published are in Zeiller (1888a: pl. 26) and Zeiller (1906: pl. 26), both under the name *Neuropteris crenulata* Brongniart. They both show bipinnate frond fragments, with intercalated pinnules on the penultimate rachis. Laveine (1967: text-fig. 6d) interprets the 1906 specimen as essentially a pinnate frond. However, the penultimate rachis in the 1888 specimen is noticeably curved, suggesting that it might be from a bipartite frond, similar to that present in many of the other neuropteroid form-genera.

The numerous records of this species from the Iberian Peninsula have been analysed by Knight (1983). He has concluded that, although they show some similarity to *S. praedentata*, they differ in having smaller, thinner-limbed pinnules with weaker crenulations on the margin, and thinner veins. They have since been transferred to a separate species, *S. wagneri* (see below). Significantly, Knight also observed that the Spanish material shared some features in common with *S. dimorpha*, providing some support for the idea that *S. dimorpha*, *S. praedentata* and *S. wagneri* cluster together to form a reasonably natural form-genus.

OCCURRENCE. (?)Saar-Lorraine (Bar), Massif Central (Bar-StC).

Sphenoneuropteris wagneri (Lorenzo) Cleal & Shute, comb. nov.

*   1980   *Mixoneura wagneri* Lorenzo: 11–13; pl. 1.

REASON FOR GENERIC ASSIGNMENT. The large, relatively lax pinnules with a wide venation.

COMMENTS. This species was established for the Spanish specimens that were traditionally assigned to '*Neuropteris*' *praedentata* (see comments on previous species).

OCCURRENCE. NW Spain (Bar-Aut).

Species of uncertain taxonomic position

Included here are those species which, although clearly circumscribed and thus 'good', cannot be readily assigned to any of the above form-genera. Cuticular evidence is lacking, and their pinnule and pinna morphologies do not provide any obvious comparison with one or other of the more completely known species.

Neuropteris bourozii Laveine

*   1967   *Neuropteris bourozii* Laveine: 152; pls 23–25.

COMMENTS. Some of the pinnules of this species show similarities to *Laveineopteris* (Laveine 1967: pl.24, fig.5), while others are of a more typical neuropterid-type (Ibid. pl.23, fig.5). Laveine (1967) assigned specimens from the Pennines Basin figured by Bolton (1926: pl. 6) to this species, but they almost certainly belong to *L. tenuifolia*.

OCCURRENCE. Franco-Belgian Basin (Duc), NW Germany (Duc).

Neuropteris cordata Brongniart

*   1831   *Neuropteris cordata* Brongniart: 229; pl. 64.
.   1890   *Nevropteris Raymondii* Zeiller: 147; pl. 9a, fig. 4.
.   1893   *Neuropteris pseudoblissii* Potonié: 137.
.   1964   *Mixoneura raymondii* (Zeiller) Wagner: 9.

COMMENTS. This species cannot readily be fitted into any of the other form-genera. The general aspect of the pinnules suggests affinities with *Neurocallipteris* or possibly even *Neuropteris*, but what little is known of the frond architecture (e.g. Langiaux 1984: fig. 111) would seem to separate it from both genera. The species is in clear need of a revision.

The type and only known specimen of *N. raymondii* Zeiller (*Mixoneura raymondii* (Zeiller) Wagner) was figured photographically by Doubinger (1956: pl. 12, fig. 3; pl. 13, fig. 1). It originated from the Mont Pel Formation in the Autun-Epinac Basin, and occurs together with specimens of *N. cordata*. The pinnules are rather smaller (*c.*16 mm long) than is typical for *N. cordata* but the venation is very similar. Doubinger (1956) claims that the veining density is higher in *N. raymondii*, but the measured value of 22 veins per cm on the pinnule margin is quite compatible with some of the smaller forms of *N. cordata* (cf. Zeiller 1906: pl. 27, fig. 3). In view of the evidence of association and of the similarity of the venation, it seems reasonable to assume that *N. raymondii* is merely a small-pinnuled form of *N. cordata*, possibly from the more distal regions of the frond.

N. pseudoblissii is still being recorded in the modern literature for specimens from the upper Stephanian with very elongate pinnules, but which are otherwise very close to *N. cordata*. Zeiller (1888a), who figured the types of Potonié's species under the incorrect name *Neuropteris blissii*, noted that isolated fragments would be difficult to distinguish, and it is also significant that the two species almost invariably occur together (e.g. see records in Doubinger 1956). There thus seems little justification for separating the two species.

The single specimen from the Duckmantian of the Pennines figured by Crookall (1959: pl. 41, fig. 5) as *N. pseudoblissii* is an indeterminable fragment, possibly of a mariopterid.

OCCURRENCE. Massif Central (StB-StC), Pyrenees (StC), Alps (StC), N. Portugal (StC).

Neuropteris duprei Laveine

*   1967   *Neuropteris duprei* Laveine: 164; pl.29, figs 1–4.

COMMENTS. This is a very distinctive species with elongate, often asymmetrical pinnules and very oblique lateral veins. The only other similar material reported from Europe are the specimens described by Němejc (1949, pl.1, figs 1–8) as *Odontopteris stradonicensis* Andrä. There is also a record from the Langsettian of NW Spain (Wagner & Bowman 1983), but it is not illustrated.

OCCURRENCE. Franco-Belgian Basin (Lan-Duc).

Neuropteris dussartii Laveine

*   1967   *Neuropteris dussartii* Laveine: 191; pl.48.

COMMENTS. Laveine argued that this species shared a number of features in common with laveineopterid species such as *L. loshii* and *L. rarinervis*. However, Laveine also pointed out certain similarities with *Neuropteris ovata*, such as the presence of a basiscopic auricle on some of the pinnules.

OCCURRENCE. South-West UK (Bol-WeD), Franco-Belgian Basin (WeD), NW Germany (WeD).

Neuropteris teberdensis Shchegolev

* 1979 *Neuropteris teberdensis* Shchegolev: 163; pl. 51; pl. 52, fig. 1; pl. 53, fig. 1.

COMMENTS. The pinnules of this very late species show a marked resemblance to *Neuropteris ovata*, suggesting that it is a true neuropterid. However, one of the specimens (Shchegolev 1979: pl. 52, fig. 1) suggests that the frond might have been only bipinnately divided, with intercalated pinnules on the primary rachis branches. This fact, together with its high stratigraphical position, suggests that the species may instead belong to *Neurodontopteris*.

OCCURRENCE. N. Caucasus (StC).

Neuropteris zeilleri de Lima

T 1864 *Neuropteris cordata* Brongniart; Göppert: 100; pl. 11, figs 1–2.

* 1890 *Neuropteris zeilleri* de Lima: 140.

COMMENTS. This species has been widely quoted in the literature as occurring in the upper Stephanian of Europe (e.g. Havlena 1953, Doubinger 1956, Wagner 1963, Vetter 1968, Wagner & Sousa 1983). As pointed out by Zeiller (1906) and Vetter (1968), however, there are problems with the typification of the species; that quoted above is the one normally accepted, but it is far from clear if de Lima regarded Göppert's specimens or his own Portugese specimens as types. The distinction from *Neuropteris cordata* is also far from clear and according to Zeiller is based mainly on the fact that there is not a single midvein, but a number of separate, fine veins lying along the long axis of the pinnules. This distinction has never been properly documented and there must be a strong suspicion that it is purely taphonomic. Whatever the outcome, however, there can be little doubt that *N. zeilleri* will end up in the same form-genus as *N. cordata*, whatever that will prove to be (see above).

OCCURRENCE. (?) Intra-Sudetic Basin (Aut), Massif Central (?StB, StC-Aut), NW Spain (StB, ?StC), N. Portugal (StC-Aut).

Nomina dubia

The first group of species included here were initially described on just one or two fragments and additional material has not been published. There is thus insufficient evidence of morphological variation to be able to recognize the species reliably, or of features such as frond architecture or epidermal structure, by which their generic position could be assertained. They are listed below without further comment.

Imparipteris flabellinervis Gothan, 1953: 59; pl. 9, figs 2–3; pl. 28, fig. 2; pl. 30, fig. 6.

Neuropteris asturiana Jongmans MS ex Wagner, 1962: 757 [nomen nudum].

Neuropteris beveridgei Crookall, 1959: 189, pl. 40, fig. 4.

Neuropteris bulupalganensis Zalessky *in* Zalessky & Chirkova, 1933: 9; fig. 1.

Neuropteris(?) delasii Zeiller, 1892: 45; pl. 8, fig. 6.

Neuropteris dispar Zeiller, 1888a: 253; pl. 29, fig. 6.

Neuropteris horrida Zeiller, 1888a: 251; pl. 32, figs 1–2.

Neuropteris jugosa Kidston ex Crookall, 1959: 164; pl. 41, fig. 3.

Neuropteris matheronii Zeiller, 1888a: 245; pl. 28, fig. 7.

Neuropteris pseudoimpar Stockmans & Willière, 1953: 235; pl. 44, fig. 2; pl. 50, fig. 12.

Neuropteris squarrosaeformis Kidston ex Crookall, 1959: 163; pl.50, fig.6.

Neuropteris subsessilis Stockmans & Willière, 1955: 14; pl. 8, fig. 1.

Neuropteris waltonii Stockmans & Willière, 1953: 227–228.

In addition to the above, there are a number of other species, for which more specimens are known, but which are still impossible at present to identify reliably. These require further comment.

Mixoneura muensterifolia Němejc

* 1949 *Mixoneura muensterifolia* Němejc: 15–16; pl. 3, figs 10–14.

. 1949 *Mixoneura grandifolia* Němejc: 18–20; text fig. 4.

COMMENTS. Němejc established this species for a number of fragments from the middle Westphalian, that were claimed to have a pinnule shape similar to *Neuropteris obliqua*, but with more flexuous veins. These are similar to the characters used to define *N. semireticulata*, of which it would be an earlier synonym. However, the illustrations used by Němejc are poor and the specimens fragmentary. It would thus be unwise to give it priority over *N. semireticulata*, at least until Němejc's species is better documented.

Němejc reported larger pinnules in close association with *M. muensterifolia*, and used them as the types of another new species, *M. grandifolia*. However, the figured specimens would seem to correspond with forma *impar*-type pinnules found in the proximal parts of the fronds of the *N. obliqua* group. It is thus almost certain that they are conspecific with the specimens that he assigned to *M. muensterifolia*.

Neuropteris arberi Crookall

* 1959 *Neuropteris arberi* Crookall: 148; pl. 50, fig. 7; pl. 51, figs 2–4.

COMMENTS. Based on three fragments, none of which show details of the apical pinnules or the pattern of lobing. Their affinities may be more mariopterid than neuropterid. Remy & Remy (1975) attempted to use this species for German specimens, but it is difficult to see how this can be justified in the light of the extremely imperfect types.

Neuropteris kosmannii Potonié

* 1903 *Neuropteris kosmanni* Potonié: 399.

T 1913 *Neuropteris kosmanni* Potonié; Gothan: pl. 47, fig. 3; pl. 50, figs 1–4.

COMMENTS. Although this species periodically re-appears in the literature (e.g. Kotasowa 1968), it has only ever been described from small fragments. They all show vaulted, extremely thick-limbed pinnules, often with a somewhat undulate margin, quite atypical for any of the neuropteroid form-genera, with the possible exception of *Margaritopteris*. In the absence of more complete material, it is impossible either to give it a useful circumscription as a species, or to determine their generic position.

Neuropteris lubnensis Havlena

* 1953 *Neuropteris lubnensis* Havlena: 153–154; pl. 6, figs
   1–2.

COMMENTS. This is based on forty-eight specimens preserved
in a sandstone, although only two were figured. They are
undoubtedly unusual, having very large pinnules (up to 4 cm
long and 2 cm wide), and do not fit into any previously
described species. However, the arenaceous matrix is far
from perfect for preserving this type of fossil, and the number
of specimens illustrated is inadequate to determine the range
of morphological variation, let alone frond architecture.
Much better material needs to be documented before any-
thing can be done with this species.

Neuropteris montana Heer

* 1879 *Neuropteris montana* Heer: 22; pl. 6, figs 22, 23.
T 1960 *Neuropteris montana* Heer; Jongmans: pl. 21, fig.
   121.

COMMENTS. From the form of the distal part of the pinna, the
type clearly belongs to a paripinnate frond, presumably of the
Potonieaceae. It is reputed to originate from the Cantabrian
or lower Barruelian, which is far higher stratigraphically than
Paripteris normally occurs. The venation is very poorly
preserved, but may be anastomosed with very elongate
vein-meshes. If so, then it may belong to *Linopteris neu-*
ropteroides (Gutbier) Potonié, 1899, which sometimes occurs
as high as Barruelian. However, the material is really inad-
equate to give an unequivocal statement on this.

ROBUSTNESS OF GENERIC TAXONOMY

The statistics of this taxonomic analysis are summarized in
Table 2 and Fig. 18. A total of 101 neuropteroid species have
been recorded from Europe over the last half century, of
which nearly a half (43·5%) are either unsatisfactory because
they are based on insufficient material, or are later synonyms
of other species. Of the remaining fifty-seven 'good' species,
all but six (10·5%) can be assigned to one or other of the 9
form-genera summarized in the early part of this paper.

The six species that cannot yet be placed in our generic
classification fall into three groups.

1. *N. cordata* and *N. zeilleri* appear closely related to each
other and it is far from certain that they are not in fact
conspecific. Although widely recorded from the Stephanian
and Autunian of France and the Iberian Peninsula, little is
known of the frond architecture and nothing of the cuticles
(the cuticles assigned to *N. cordata* by Barthel, 1976, in fact
belong to *Neurodontopteris auriculata* – see above).

2. *N. duprei* has unusual, asymmetrical pinnules unlike
any of the other species included in this analysis; in fact they
are different from any type of foliage previously assigned to
the trigonocarpaleans. It may well belong to a new form-
genus, but details of the frond architecture and/or cuticles will
be needed before any decision on this can be made.

3. From the general aspect of the pinnules, it is likely that
N. bourozii, *N. dussartii* and *N. teberdensis* belong to either
Neuropteris, *Laveineopteris* or *Neurocallipteris*. Again, evi-
dence of frond architecture and/or cuticles will be needed
before a decision can be made on their classification.

In conclusion, the analysis has allowed us to see where the
main gaps are in our knowledge of these fossil fronds. In
particular, the 6 species that cannot currently be assigned
need to be further investigated. Nevertheless, we believe that
the results support the essential robustness of our generic
classification of neuropteroid fronds, and points to it being a
potentially useful tool for understanding more clearly the
distribution of these plants.

DIVERSITY ANALYSIS

Diversity of the neuropteroids as a whole

As a by-product of this study, whose original goal was merely
to ascertain the robustness of the generic classification of
neuropteroid fronds, we have built up a database of the
stratigraphical and geographical distribution of species within
Europe. This would appear to invite further analysis of
diversity variations. Diversity analysis has become a popular
pursuit in recent years, but can be prone to serious problems

Fig. 18   The robustness of the taxonomy of neuropteroid fronds. (a) The proportions of synonyms, inadequately described and 'good' species
among all those neuropteroids used since 1940. (b) The proportion of the 'good' species belonging to each of the form-genera.

Table 2 Statistics of neuropteroid taxonomy

Form-genera	No. of species	% (Total)	% (Good)
Laveineopteris	9	8·91%	15·79%
Macroneuropteris	4	3·96%	7·02%
Margaritopteris	1	0·99%	1·75%
Neuralethopteris	7	6·93%	12·28%
Neurocallipteris	3	2·97%	5·26%
Neurodontopteris	1	0·99%	1·75%
Neuropteris	15	14·85%	26·32%
Paripteris	5	4·95%	8·77%
Sphenoneuropteris	6	5·94%	10·53%
Uncertain affinities	6	5·94%	10·53%
Inadequately circumscribed	17	16·83%	
Synonyms	27	26·73%	
Total 'good' species	57	56·44%	
Total 'bad' species	44	43·56%	
Grand total	101	100·00%	

due at least in part to the tendency to use data trawled uncritically from the literature (cf. comments by Cleal 1988). Our database, although based only on a small range of species, at least has the merit of having been critically compiled.

To this end, a tabulated set of statistics has been compiled to represent diversity, first-appearances and extinctions for each stage (Table 3). This has been done separately for each of the form-genera, as well as for the group as a whole (including those species unassignable to any of the form-genera).

The diversity of the group as a whole follows a fairly simple pattern, showing a marked peak in the Westphalian, followed by a rapid decline and then a subsidiary peak in the upper Stephanian (Fig. 19A). The Westphalian peak would seem to be confirmed by observations made by Boulter *et al.* (1988) on diversity changes in the wider plant adpression record for the palaeoequatorial belt. It almost certainly reflects variations in the available non-marine strata in Europe; Niklas *et al.* (1980, p. 29) demonstrated that 98·5% of plant fossil diversity (at least between the Carboniferous and Jurassic) can be accounted for by this single factor. Numerical data on the available strata in each stage are not available for Europe. However, our observations would seem to confirm the general impression that delta-plain, fluvio-lacustrine deposits, which presumably reflect the habitats favoured by the plants producing these fronds, are at a maximum in the Westphalian and upper Stephanian, with a low in the Cantabrian and, to an extent, the Baruellian.

Figs 19B and 19C show the patterns of appearances and extinctions per stage, both corrected for variation in the length of the stage. These show curves with a similar double-peaked form to the diversity curve. A broad correlation between species turn-over and diversity is not surprising. However, the species profit/loss curve (Fig. 19D) shows a more interesting pattern. Up to the Kinderscoutian the situation is relatively stable, but at higher stratigraphical levels there are major fluctuations. Peaks occur in the Kinderscoutian, Langsettian and Baruellian/Stephanian B. The first of these can be correlated with the first appearance of large-scale deltas across northern Europe; the second the

proliferation of coal-swamp conditions on the delta-tops; and the third the expansion of intra-montane basins in central and southern Europe. The trough in the Cantabrian presumably reflects the change-over from predominantly paralic to predominantly intra-montane conditions over much of Europe.

So, the diversity of the neuropteroids as a whole is merely a function of the general diversity of the tropical swamp vegetation. If the form-genera outlined earlier in this paper have any basis in the genetic relationships of the parent plants, diversity patterns of the individual form-genera may tell a different story. Fig. 20 shows the diversity curves of six of the most abundant of the form-genera plotted separately. This clearly shows that the story is far more complex. However, the style of analysis dealt with so far in this paper is not really suitable for uncovering the more detailed distributional patterns. For this, we need to look at the detailed variations in diversity of the species within each of the form-genera.

The problem here is the limited amount of suitable data available. There have been studies documenting the quantitative stratigraphical variations of different species, such as by Davies (1929). However, such work is mostly old, largely unillustrated and uses unreliable taxonomy. Also, as pointed out by Scott (1985), there are serious weaknesses with the sampling that was usually employed. Scott himself suggested that quadrat analysis, similar to that sometimes used to study living plant ecology, could produce more reliable results. However, while quadrat analysis might prove valuable in the detailed relationship between facies and plant fossils at a specific locality, it would need a considerable number of such studies before it would reveal any meaningful stratigraphical patterns of plant fossil distribution.

We have instead adopted an alternative approach, by looking at the numbers of localities from where a species is recorded at different stratigraphical levels. To do this, it was decided to restrict the analysis to one particular area, which would help minimize potential palaeolatitudinal variations. The area should have numerous records spread over a reasonably long stratigraphical range. The data should also preferably be based on identifications made by a single authoritative palaeobotanist, thus minimizing the potential for subjective variations in identification. In fact, only one area was found to have all these virtues, namely the Franco-Belgian Basin, through the monographic study by Laveine (1967).

Species diversity analysis (Franco-Belgian Basin)

Laveine's (1967) monograph provides a taxonomically reliable record of most of the neuropteroid species found in the paralic belt between the Kinderscoutian and Westphalian D. For each species, he individually lists the localities where they are found in the Nord-Pas-de-Calais Coalfield, divided stratigraphically into lower, middle and upper divisions of the formations there. Using this data, we have plotted the diversity curves for each species of four of the form-genera (Figs 21–23).

Neuropteris (Fig. 21). These 7 species appear to fall into two groups. The early group consists of *N. obliqua*, *N. heterophylla*, *N. ghayei* and *N. willieri*, which occur predominantly in the Langsettian and basal Duckmantian (in Belgium, *N. obliqua* is reported to extend down to the Marsdenian, but the French records on which the present
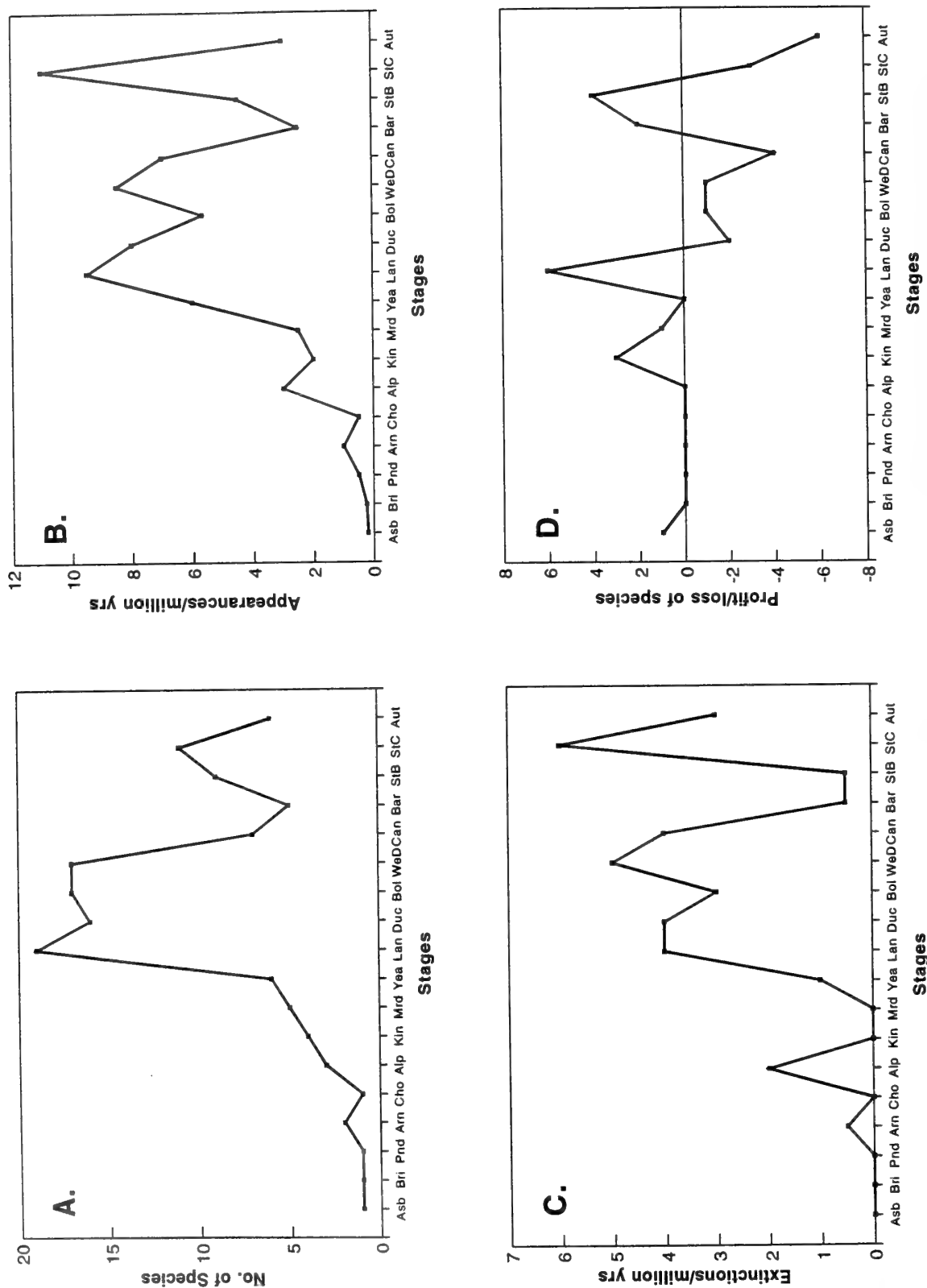
Fig. 19 Diversity curves for the group of neuropteroid species as a whole: (a) number of species in each stage; (b) number of species appearing per million years in each stage; (c) number of species extinctions per million years in each stage; (d) profit/loss of species in each stage.

Table 3 Diversity variations in Neuropteroid genera.

Stage	Laveineopteris N	F	TF	L	Macroneuropteris N	F	TF	L	Neuralethopteris N	F	TF	L	Neurocallipteris N	F	TF	L	Neuropteris N	F	TF	L	Paripteris N	F	TF	L	Spenoneuropteris N	F	TF	L	Total N	F	TF	L
Asb																	1	1	13·0										1	1	13·0	
Bri																	1												1			
Pnd																	1												1			
Arn																	1			1									2	1	5·0	1
Cho									1	1	10·0	1																	1			
Alp									1								1	1	0·5	1									3	2	0·5	
Kin									3	2	5·0						1	1	10·0		1	1	8·0						4	3	5·8	
Mrd									3								2	1	5·0		1								5	1	2·0	2
Yea									3								2				1								6	1	1·7	
Lan	3	3	4·3		1	1	7·0		6	4	0·8	6					4	2	1·5	1	2	1	3·0		1	1	0·2	1	19	14	2·4	1
Duc	5	2	0·6	2	1												4	2	3·5	2	4	2	5·0	2					16	6	2·3	8
Bol	5	2	3·1	3	1												6	3	1·5	3	3	1	2·0	3					17	8	2·4	8
WeD	3	1	0·2	2	4	3	1·3	2					1	1	8·0		7	4	2·7	5					1	1	7·0		17	9	1·9	9
Can	1			1	2			2					1				2			1					1				7			10
Bar													2	1	5·0										3	2	7·5	1	5	3	6·5	4
StB													3	1	5·0										2				9	5	3·4	1
StC													3			1	1	1	0·2	1					4	2	0·2	3	11	3	0·4	6
Aut													2			2	1			1					1			1	6			6

N = Number of species present in stage.
F = Number of first appearances in stage.
TF = Average duration (in million years) of species first appearing in stage.
L = Number of extinctions in stage.
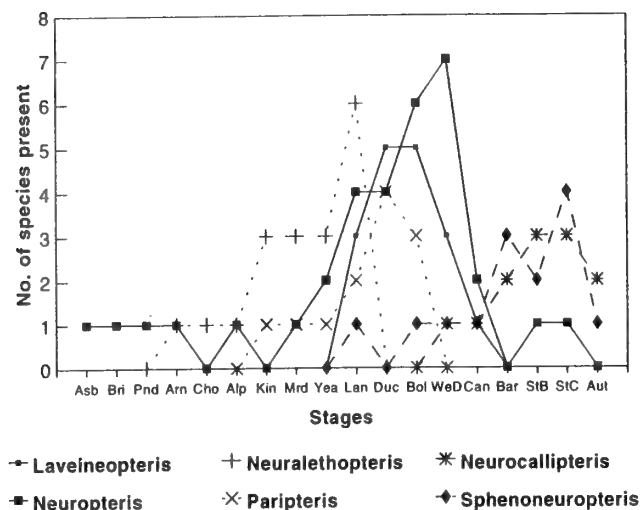
Fig. 20 Stratigraphical diversity of six of the more abundant neuropteroid form-genera, showing complexity hidden by generalized graph in Figure 19a.

analysis is based only show it as far back as the Langsettian). It then undergoes a significant decline in the lower Duckmantian. Only one of the species extends much beyond the middle Duckmantian, and that is what is referred to in the chart as the *N. obliqua* group. This pattern seems to be in general agreement with what is seen in areas other than the Franco-Belgian Basin.

As with the other neuropterids, *N. obliqua sensu stricto* undergoes a marked decline in the lower Duckmantian. However, in the upper Duckmantian there is the start of a progressive change in the venation, which becomes more flexuous and eventually culminates in the anastomosed-veined form known as *Reticulopteris* Gothan. Details of this gradual change in venation through the Duckmantian and Bolsovian have been documented by Josten (1962), and the possible adaptive advantage of this style of venation is discussed by Zodrow & Cleal (1993). This morphological change is accompanied by a proliferation of the group of species, especially in the Bolsovian.

The abundance of the *N. obliqua* group then undergoes a dramatic collapse in the topmost Bolsovian and it eventually becomes extinct in the upper Westphalian D. This collapse in abundance coincides approximately with the appearance of the second group of neuropterids at the base of the Westphalian D. In the Franco-Belgian Basin, this consists of just one species, namely *N. ovata*, but elsewhere in Europe there are other, very similar species which come in at about the same level (*N. flexuosa, N. plicata* and *N. ervedosensis*). This is near the top of the Upper Carboniferous succession in this basin and so provides no direct evidence of the diversity of these neuropterids at higher levels. However, in other areas such as South Wales (Cleal 1978) and NW Spain (Wagner *et al.* 1983, Wagner & Alvarez-Vázquez 1991) it is clear that the group continues to be abundant at least through the Westphalian D and Cantabrian, and in some cases beyond.

There is no direct evidence from the Franco-Belgian Basin of the phylogenetic origins of the *N. ovata* group. There is a possible precursor in the Bolsovian of the Intra-Sudetic Basin (*N. praeovata*), but this throws little light on potential ances-
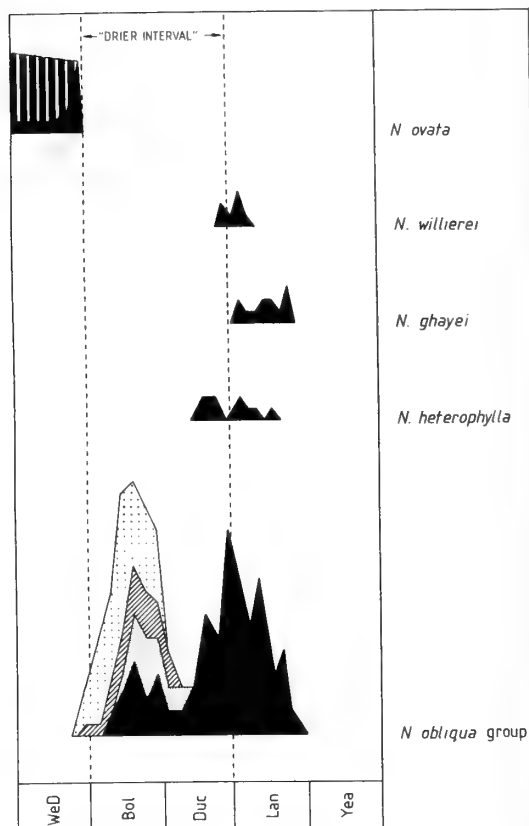
Fig. 21 Detailed abundance variations of *Neuropteris* species, plotted against stages (using abbreviations shown in Fig. 2). In the graph of the *Neuropteris obliqua* group, black represents *N. obliqua*, fine stippling *N. parvifolia*, diagonal hatching *N. semireticulata*, and coarse stippling *Reticulopteris muensteri*. Based on data from Laveine (1967), determined from the Franco-Belgian Basin. The shaded expansion of the *N. ovata* curve reflects its proliferation in other areas.

tors. Almost certainly, the group evolved in an extra-basinal habitat, possibly from a *N. heterophylla*-like ancestor.

Laveineopteris (Fig. 22). The laveineopterids may be divided into two main groups: those with larger pinnules (the *L. tenuifolia/loshii* group) and those with smaller pinnules (the *L. rarinervis* group). The larger pinnuled-group first appears in the Langsettian with *L. loshii*, which reaches its acme in the upper Langsettian. At about the Langsettian-Duckmantian boundary, however, it undergoes a significant decline in abundance, and is replaced by a number of species with more elongate pinnules (*L. tenuifolia, L. hollandica, L. jongmansii, L. morinii*). These species, especially *L. tenuifolia*, remain abundant and characteristic elements of the Duckmantian and Bolsovian, but then towards the top of the Bolsovian decline sharply to become extinct in the lower Westphalian D.

The *L. tenuifolia* group shows a reduction in abundance at about the Duckmantian-Bolsovian boundary, but is otherwise an important and characteristic element found in those stages. However, towards the top of the Bolsovian it undergoes a second and this time terminal decline, finally becoming extinct in the basal Westphalian D.
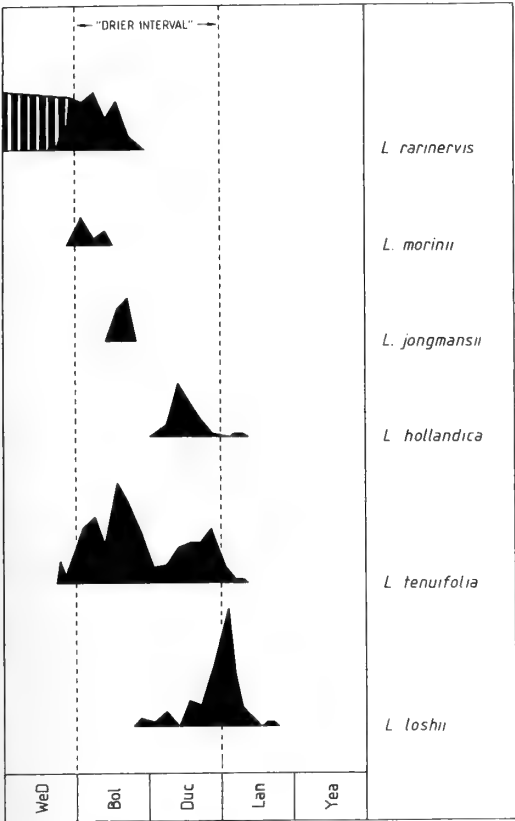
Fig. 22 Detailed abundance variations of *Laveineopteris* species, plotted against stages (using abbreviations shown in Fig. 2). Based on data from Laveine (1967), determined from the Franco-Belgian Basin. The shaded expansion of the *L. rarinervis* curve reflects its proliferation in other areas.

Fig. 23 Detailed abundance variations of *Neuralethopteris* and *Paripteris* species, plotted against stages (using abbreviations shown in Fig. 2). Based on data from Laveine (1967), determined from the Franco-Belgian Basin.

The *L. rarinervis* group of very small-pinnuled species shows a somewhat different distributional pattern. In the Franco-Belgian Basin it starts in the Bolsovian, having possibly originated from the slightly older *L. nicolausiana*. It proliferates during the Bolsovian. In the lower Westphalian D it appears to decline in the Franco-Belgian Basin, but this is symptomatic of it being at the top of the Upper Carboniferous succession here; elsewhere in the paralic belt of coalfields, it continues to be abundant through into the Cantabrian.

Neuralethopteris (Fig. 23). It is well known that this form-genus is restricted to the Namurian and Langsettian, a point which is borne out by the Franco-Belgian data. The only other point of possible significance is that, compared with many of the other neuropteroid taxa whose extinctions are normally marked by a gradual decline in abundance, the extinctions of most of the neuralethopterids is characterized by a sudden proliferation followed by a sudden decline.

Paripteris (Fig. 23). According to Laveine *et al.* (1989), the plant that bore paripterid fronds migrated from China to Europe in the early Namurian. Elsewhere in Europe, it first appears in the Kinderscoutian, while in the Franco-Belgian Basin its lowest occurrence seems to be in the Marsdenian. The stratigraphically lowest species is *P. gigantea*, which

extends through the rest of the Namurian, and proliferates in the Langsettian.

At about the start of the Duckmantian, *P. gigantea* starts to show a progressive decline, and is replaced by a new set of species (*P. pseudogigantea*, *P. linguaefolia*). These remained important elements of the Duckmantian and Bolsovian equatorial floras, except for a brief and temporary decline near the Duckmantian-Bolsovian boundary. Towards the top of the Bolsovian, however, these paripterids start a more significant reduction in abundance, and they eventually become extinct just below the base of the Westphalian D.

Macroneuropteris. Only one species of this form-genus occurs in the Franco-Belgian Basin (*M. scheuchzeri*), and so it has not been shown on the charts. The lowest occurrence of *M. scheuchzeri*) here is in the upper Duckmantian, although elsewhere it has been documented from as low as the upper Langsettian (Pennines Basin – Cleal 1979). It reaches an acme in the upper Bolsovian and then appears to decline. However, it should be noted that elsewhere it remains an abundant species through to the Cantabrian.

Palaeoecological controls on species distributions

From the above analysis of species distributions, a clear pattern has emerged. Most significantly, there are two major stratigraphical levels where changes occur:

1. The Langsettian-Duckmantian boundary. This marks (a) the extinction of *Neuralethopteris*, (b) the start of the decline of the early group of *Neuropteris* species, (c) the transition from *Laveineopteris loshii* to the more elongate-pinnuled laveineopterids (*L. tenuifolia* group), and (d) the transition from *Paripteris gigantea* to *P. pseudogigantea* and *P. linguaefolia*.

2. The Bolsovian – Westphalian D boundary. This marks (a) the extinction of *Paripteris*, (b) the decline and eventual extinction of *Laveineopteris*, (c) the decline and eventual extinction of *Reticulopteris* and *Neuropteris semireticulata*, and (d) the sudden appearance and proliferation of the second group of *Neuropteris* species allied to *N. ovata*.

It is clearly tempting to search for a palaeoecological explanation for these two 'events', and we believe that such an explanation can be found in the results of the coal ball analyses summarized by DiMichele *et al.* (1985). Their model was based on a number of different lines of evidence from the peat-accumulating habitat vegetation, including species composition and the extent of the peat deposits. It seemed to show that through the Late Carboniferous edaphic conditions in the swamps would vary, with some periods of time being slightly drier than others. In the middle Westphalian, for instance, they found that some of the arborescent lycophyte genera declined (e.g. *Lepidophloios*, *Diaphorodendron*) and there was a corresponding increase in the *Mesoxylon/Mitrospermum*-type cordaites, which they interpreted as indicating rather drier conditions. From the point of view of our study this is significant, as this drier interval ranged from about the start of the Duckmantian to the end of the Bolsovian, which exactly fits with the neuropteroid distributional patterns that we have found. To make this clear, we have plotted this 'drier interval' on the distributional charts in Figs 21–23.

If the correlation between the coal ball data and the neuropteroid distributions can be accepted, it has a number of significant results:

1. *Neuropteris* species, except for those that developed a significantly flexuous to pseudoanastomosed venation, were mainly restricted to the wetter interval.

2. The development of flexuous, pseudoanastomosed and eventually reticulate veining in *Neuropteris/Reticulopteris* occurred when there was a change to drier conditions. It would seem to have been caused by a fundamental change of the genotype as, when conditions reverted to being wetter in the Westphalian D, *Reticulopteris* was unable to reverse the change.

3. The earliest known laveineopterid (*L. loshii*) was commonest at the time of wetter conditions in the Langsettian. This was replaced as the dominant member of the form-genus by the more elongate pinnuled forms (*L. tenuifolia, L. jongmansii, L. hollandica, L. morinii*) when conditions became drier, at about the Langsettian-Duckmantian boundary. The change was gradual and some pockets of *L. loshii* persisted through to the early Bolsovian (for instance, the well-known Duckmantian flora of the Barnsley Seam of Yorkshire, U.K.).

4. The reversion to wetter conditions in the Westphalian D coincided with the rapid decline and eventual extinction of the elongate pinnule forms of laveineopterid.

5. The small pinnule forms of *Laveineopteris* (*L. rarinervis*) appear not to be constrained by the same environmental factors as the rest of the species. They first appeared in the

drier interval of the middle Westphalian, but seemed equally at home in the wetter conditions of the Westphalian D. *Macroneuropteris* would seem to have been similarly unaffected by the environmental change in the early Westphalian D.

6. Like the laveineopterids, there was just one paripterid species in the first wet interval (*P. gigantea*). It appears to have many features in common (although it is not exactly the same species – Laveine, pers. comm., 1992) with the paripterids found in the upper Visean of China, which are thought to represent the ancestral stock of this form-genus (Laveine *et al.* 1989, 1992). According to the Laveine *et al.* model, paripterids spread out westwards from China during the very late Visean and early Namurian, along the northern coast of the Proto-Tethys Ocean. It is likely that these early paripterids favoured the wetter habitats of the lower delta plains. It would thus not be surprising that the earliest paripterid in Europe (*P. gigantea*) would also favour wetter habitats.

7. Again, like the laveineopterids, on the change to drier conditions in the early Duckmantian, the early species (*P. gigantea*) declined rapidly and was replaced by *P. pseudogigantea* and *P. linguaefolia*. Both of these later species may have been adapted to the drier conditions of the middle Westphalian and did not survive the return of wetter conditions in the Westphalian D. This resulted in the extinction of the whole form-genus, although the group as a whole persisted through to the lower Stephanian in the form of its reticulate-veined cousin *Linopteris*.

8. The upper Duckmantian and lower Bolsovian has numerous marine bands, indicating a change to lower delta plain conditions (Guion & Fielding 1988). This coincides with a temporary decline in abundance of both the laveineopterids and paripterids, which then recovered in abundance when middle delta plain conditions returned in the middle and upper Bolsovian. The levees were almost certainly of lower topography in a lower delta plain setting, and thus represented wetter conditions than the levees of the upper Langsettian and lower Duckmantian. This seems to confirm that these mid-Westphalian laveineopterids and paripterids were more abundant in drier conditions.

9. The neuralethopterids appear to have been totally restricted to the wetter conditions prevalent in the Langsettian. Unlike the laveineopterids and paripterids, they seemed unable to adapt to the change to drier conditions in the Duckmantian and became extinct.

The correlation between these events, identifiable in the adpression record, and the changes in the coal-swamp petrifactions is remarkable, but it is evident that they are not sharp events. For instance, the start of drier conditions probably ranged through the lower part of the Duckmantian, while the return of wetter conditions gradually developed from the topmost Bolsovian to the lower Westphalian D. This is suggested by the moisture curve given for coal-swamps by DiMichele *et al.* (1985, fig. 8.1), but the much better evidence that we have from the adpression record demonstrates it far more clearly.

DiMichele *et al.* (1985) argue that the 'wetter' and 'drier' conditions in their model refer to the edaphic conditions, which in turn were responses to variations in climate. However, whether these climatic changes were in the swamp forests themselves, or in the hinterlands that supplied the river-waters is not clear. That the changes can be identified

over wide geographical areas in North America and Europe suggests that climate may well have been a major factor. However, the temporary decline of the laveineopterids and paripterids in the upper Duckmantian and lower Bolsovian, suggests that the topography of the levees may also have been a controlling factor.

Species diversities in other areas

As already stated, it is impossible to do the same type of detailed diversity analysis in the other areas as we have done in the Franco-Belgian Basin. However, there are a few points which can be made on the distributions in some of these other places.

It is well known that in Saar-Lorraine, *Laveineopteris tenuifolia* becomes prematurely extinct in the upper Bolsovian (e.g. Laveine 1989). This is normally interpreted as a response to an environmental change in this basin, represented by a predominantly arenaceous interval known as the Geisheck Formation. From what we have learnt in the Franco-Belgian Basin, it is tempting to suggest that the Geisheck Formation represents rather wetter conditions to that represented in the underlying Sulzbach Formation, in which *L. tenuifolia* occurs commonly.

Macroneuropteris scheuchzeri also becomes prematurely extinct in the Geisheck Formation of the Saar-Lorraine (Laveine 1989). This might be regarded as unexpected, as macroneuropterids in the Franco-Belgian Basin seem relatively tolerant of environmental change. However, Bertrand (1930) suggested that the Saar-Lorraine representative of this form-genus might not be taxonomically identical to that seen in the paralic basins, having somewhat smaller pinnules with only one (rather than two) basal lobe. Although this view has not been widely accepted in the literature, the differences in response to environmental change may support Bertrand's original contention.

Over much of Europe, *Neuropteris sensu stricto* is rare in the Duckmantian and Bolsovian. A significant exception is in NW Spain, where *N. resobae* occurs abundantly in the Duckmantian Curavacas Formation (Cleal 1981). This still fits in with the general pattern, however, as the Curavacas Formation is a unit of fluviatile deposits in an otherwise marine succession (Martínez García *et al. in* Martinez Diaz 1983) and would thus presumably have wetter edaphic conditions than present in the coalfields of the paralic belt.

Over much of Europe, *Neuropteris sensu stricto* undergoes a significant decline in the lower Stephanian. This is in agreement with the DiMichele *et al.* (1985) model, as they claim that a second (and this time more significant) drier interval started in the Cantabrian or early Barruelian in the coal-swamp habitats. In a few parts of Europe, however, *Neuropteris* remains a significant component in the upper Stephanian, such as Gard and La Mure (two of the coalfields of the Massif Central), NW Spain, N. Caucasus, Donets and the Alps. This may indicate that these areas were environmentally wetter compared with the other parts of Europe and the paralic coalfields of North America.

In most of the other parts of Europe, *Neurocallipteris* is the dominant neuropteroid form-genus in the drier interval of the Stephanian. At least some also extend up into the Autunian, which DiMichele *et al.* (1985) claim represents a return to wetter conditions. However, it is far from clear that these basal Permian beds are indeed wetter and, at least in Europe, not supported by the increasing presence of red-beds.

Table 4 Results of regression and correlation analyses of extinction (L) rates against numbers of species present (N).

	No. of species of same form-genus	Total No. of species
Regression equation	L=0·57N+0·22	L=0·13N+0·48
Correlation coefficient (r)	0·7807	0·5402
Level of confidence that correlation is significant	99·99%	99·47%
Coefficient of determination	60·94%	29·18%

Species diversity and survival

We have so far indicated that at least some of the variation in diversity within the neuropteroid fossil record can be correlated with Palaeozoic climatic fluctuations, and with variations in the volume of suitable strata. However, it is to be expected that other factors may have had a role. One in particular, which our data is suitable to test, is the degree to which extinction rates were controlled by competition.

This has been tested by a regression and correlation analysis of the numbers of species present in each stage against the number of species of each form-genus that become extinct in that stage. Two separate analyses were performed, one using the total number of species present as the independent variable, and the other using the number of species of the particular form-genus present. In this way it was hoped to determine whether competition within a form-genus was a more important factor in determining extinctions than competition generally within the neuropteroid complex as a whole.

The results are summarized in Table 4 and Fig. 24. The first thing that is evident is that extinctions are significantly correlated with both the number of species of the same form-genus and the total number of species. However, the level of significance is much higher in the analysis using the number of species of the form-genus. Also, the coefficient of determination (the proportion of the variance in extinction rates due to variations in species numbers) is much greater; nearly two-thirds of the variance in extinctions could be accounted for by the number of species of the same form-genus present, while less than a third is accounted for by the total species numbers.

From this, we conclude that competition was an important factor controlling extinction rates of these plants, and that it was greater between species of the same form-genus than within the neuropteroid complex as a whole. The fossils represent plants that grew in a fairly narrow band of habitats and so some level of competition would be expected between most of the elements represented. However, in such a setting it would seem reasonable to expect that competition would be greatest between those species that were closest genetically. In this light, it would seem that the form-genera outlined in this paper truly reflect the genetic relationships between the parent plants, and thus support the essential robustness of the classification.

PALAEOPHYTOGEOGRAPHY

All of the records analysed in this paper originate from what
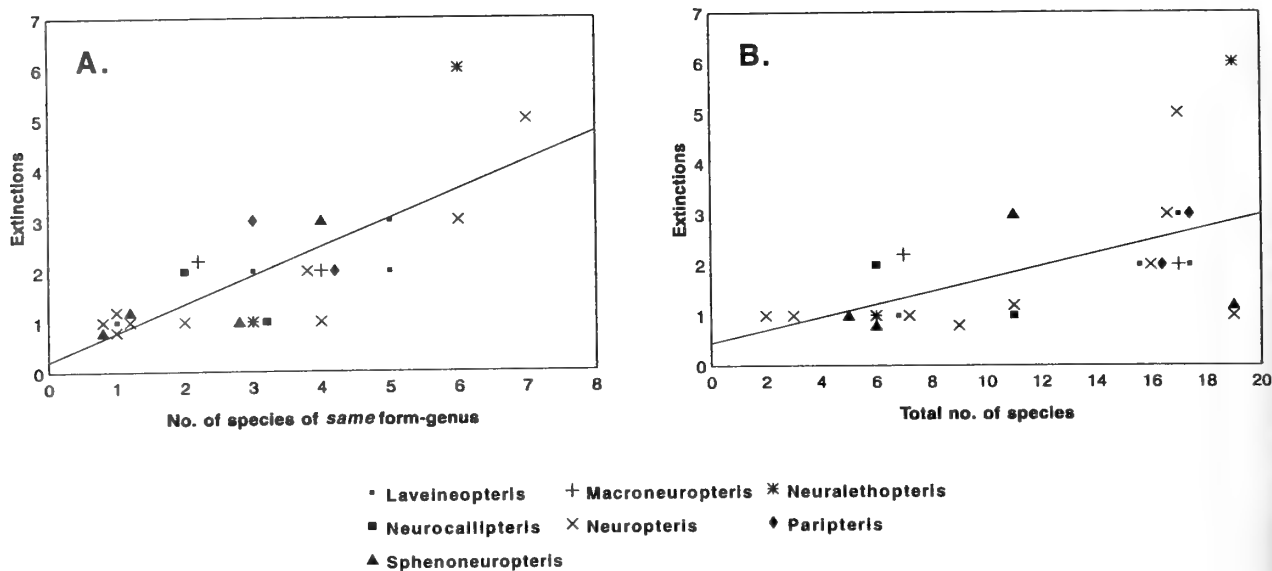
Fig. 24 Regression of extinction rates against species numbers (parameters L against N of Table 3); (a) regression against number of species of same form-genus; (b) regression against total number of neuropteroid species.

Cleal & Thomas (*in* Cleal 1991) refer to as the Europe Palaeoarea, one of the subdivisions of the Eurameria Palaeo-kingdom. There have been suggestions that this phytochorion can be further subdivided based on the plant fossil record (e.g. Gothan 1954). To investigate this possibility, we have examined our data using cluster analysis, to see if any palaeophytogeographical structure can be discerned. Our data is obviously not entirely suited to such an analysis, as it only represents a small portion of the total fossil assemblages. On the other hand, our data has the merit of having been critically assessed, and is thus preferable to some of the other recently published palaeogeographical analyses, based on uncritical literature trawls.

The database

Initially, we attempted to look at the data as a whole, using an algorithm that could account for empty data points. This was so the analysis could take into account species being sometimes absent from an area merely because there is no strata of the appropriate age there, rather than there being any fundamental phytogeographical reason. However, the results were disappointing, revealing little structure that could be related to the geographical distribution of the areas. It seemed a strong possibility that the empty data points may have significantly distorted the results.

To overcome this, the data was split into five, stratigraph-ically separate blocks. This reduced the number of empty data points to a much lower and acceptable level. It also allowed us to see if there was any stratigraphical variation in the geographical patterns. The starting-point was taken at the Chokierian, as there were too few neuropteroid species at lower levels to provide any meaningful results.

Chokierian – Yeadonian. This corresponds to most of the Namurian and includes records from 11 areas. *Margarito-pteris multivenosa* and *Neuropteris bohdanowiczii* were removed from the original data matrix. These species are only known from the Alportian, and strata of this age are

absent in 5 out of the 11 areas. It was thought that might seriously distort the results. This left 6 species, on which the clustering was based.

Langsettian. Originally 15 areas were clustered based on 18 species. However, the records for South Limburg were omitted, in order that this analysis would be in conformity with that for the next stratigraphical interval (see below).

Duckmantian – Bolsovian. Originally 14 areas were clus-tered based on 24 species. The initial result showed a major discrepancy with the position of South Limburg, which appeared to cluster at a low level with Turkey, South Spain and the Alps, rather than with the other areas of the paralic belt, as would be expected. On examining the data matrix, it seemed likely that this might be due to the inadequacy of the data from South Limburg, and so we decided to omit it from the analysis (and in consequence from that of the Langset-tian).

Westphalian D – Cantabrian. 15 Areas were clustered initially based on 14 species. The results were initially unsat-isfactory, showing what seemed to be a strong 'chaining' pattern, indicative of poor structure in the data. However, by combining the records of *Neuropteris plicata* with *N. ovata* and of *Laveineopteris piesbergensis* with *L. rarinervis*, a rather better structure became evident (the taxonomic ratio-nale for combining these species can be found in the system-atic section of this paper, although at this stage we are reluctant to make formal proposals of synonymy until the type material is subjected to a more rigorous morphological investigation).

Barruelian – Autunian. This corresponds to most of the Stephanian plus the basal Permian. The initial data set consisted of 10 localities and 14 species. However, Saxony and the Pyrenees were excluded, as they only contain records from the Autunian, and would thus distort the analysis. Also the record of *Macroneuropteris scheuchzeri* from the Inter Sudetic Basin, and of *Neuropteris schaeferi* from Saar

Lorraine were excluded. There are doubts about the reliability of the former record (see comments in systematics section) and the latter is based only on a single small fragment. The final analysis was thus run on 8 localities using 12 species.

Results

The dendrograms produced by the five analyses are shown in Fig. 25. Up to the Westphalian D, a relatively simple pattern can be seen. Many areas contain neuropteroid assemblages of relatively low diversity, in the Namurian consisting of *Neuralethopteris schlehanii* and *Paripteris gigantea*, these being supplemented by *Neuropteris obliqua* in the Langsettian. In the Duckmantian and Bolsovian, *N. schlehanii* disappears from these low diversity assemblages, and *P. gigantea* is replaced by *P. linguaefolia*. Against this background of low diversity assemblages, however, there are two assemblage-groups that are of significantly higher-diversity and, perhaps significantly, correlate with the areas of greatest coal production. These are shaded on the dendrograms, and may be summarized as follows.

1. The Paralic Belt assemblages. These include the most diverse and abundant assemblages of neuropteroids, and consistently cluster together with Jaccard Coefficients of 45 or more from the Namurian to the Bolsovian. In the Namurian it includes most assemblages of northern, central and eastern Europe, although there is some suggestion that there is an area of even greater diversity, particularly of neuralethopterids, in France-Belgium, NW Germany, U. Silesia and N. Caucasus. In the Westphalian, however, the group as a whole is limited to the paralic-belt coalfields of northern Europe (NE Germany and Lublin are not included in the Langsettian, but this may merely reflect the limited data available from these areas).

2. The intra-montane basin assemblages. Assemblages from Saar-Lorraine and the Intra-Sudetic basins take on a distinctive character in the upper Duckmantian and Bolsovian. While including some taxa also found in the paralic belt assemblages, many important constituents of the latter are missing (e.g. *Paripteris pseudogigantea*, the *Neuropteris obliqua* group, *N. heterophylla*, and *Laveineopteris rarinervis*).

The assemblages from the Iberian Peninsula also have a distinctive character, usually clustering quite separately from the rest of the areas analysed. Examining the database in detail shows that they are mainly of very low diversity but, at least in the Duckmantian-Bolsovian, include some endemic taxa (*Laveineopteris guadiatensis*, *Neuropteris resobae*). A further investigation into the Namurian and lower Westphalian neuropteroids of Iberia may well produce interesting results.

In the Westphalian D the pattern breaks down at lower stratigraphical levels. Most areas form a relatively amorphous group, which includes much of the old paralic belt, together with the Intra-Sudetic Basin, NW Spain, Turkey and N. Caucasus. The chaining structure evident in this cluster in the dendrogram suggests that there is some non-homogeneity within the group of areas, but that no clear subgroups are recognizable (although, the distinctive SW UK assemblages with *Neuropteris flexuosa* and *Macroneuropteris macrophylla* are positioned at one end of the chain). This partial reduction in palaeophytogeographical provincialism appears to correlate with the withdrawal or reduction of marine influence

from most of Europe (e.g. there are no marine bands above the middle Bolsovian in the paralic belt), and thus the disappearance of the marked distinction between the paralic and intra-montane basins. The only notable exceptions to this pattern in the Westphalian D are Saar-Lorraine (it no longer clusters with the Intra-Sudetic Basin) and the highly distinctive Zwickau assemblages.

In the Barruelian to Autunian, the cluster of areas with most diverse assemblages again seems to correlate with the major coal-producing areas, in particular the Massif Central, NW Spain and the Intra-Sudetic Basin. Saar-Lorraine seems to maintain its distinctive character, while N. Caucasus has clustered quite separately because of the presence of a number of apparently endemic taxa (although it has to be recognized that the palaeobotany of this area is far from well documented).

In conclusion, the most diverse Namurian to Bolsovian assemblages occur in the coal-bearing paralic belt of northern Europe. The coherence of this group of areas breaks down in the Westphalian D, possibly as a result of the disappearance of marine influence in these areas. In the Stephanian, a second cluster of high-diversity areas appears in the intra-montane coalfields of central and southern Europe. Saar-Lorraine (together for a time with the Intra-Sudetic Basin) retains a distinct character from these high-diversity areas, as does the short-lived Zwickau Coalfield. In general, therefore, the distribution of the neuropteroid complex supports the conclusions of Gothan (1954), that there is a clear-cut distinction between the plant fossil assemblages of the paralic and intra-montane basins. It might be tempting to use the results to justify a formal palaeophytogeographical subdivision of the Europe Palaeoarea into palaeoprovinces. However, such a move would be premature before other plant fossil groups have been subjected to similar analyses.

Endemism of individual form-genera

While there is clearly significant variation in the geographical distribution of individual species, the same is not, on the whole, so for the form-genera. Particularly the commoner form-genera (*Neuralethopteris, Paripteris, Neuropteris, Laveineopteris*) appear to be fairly evenly distributed. The only significant exception seems to be *Sphenoneuropteris*, which, throughout its range, has only been found in intra-montane basins. *Neurocallipteris* is also mainly restricted to intra-montane basins, but this is almost certainly just a function of it being primarily a Stephanian and Autunian taxon, in which paralic basins had all but ceased to exist in Europe.

Neuropteroids from outside Europe

This study has been exclusively on records from Europe, this being where these fronds are best known. However, there are records from other areas of the world, which we will discuss briefly here.

North America. The Carboniferous of eastern and central North America belongs to the Eurameria Palaeokingdom. It is to be expected therefore that similar if not identical neuropteroids would be found here as in Europe. The problem is that, other than in the Maritime Provinces of Canada (e.g. Bell 1938, Cleal & Zodrow 1989), the Carboniferous adpressions of North America have been very little

Fig. 25 Cluster analyses using geographical distributions of neuropteroid species (see text for details of methods of analysis); (a) Chokierian to Yeadonian; (b) Langsettian; (c) Duckmantian to Bolsovian.
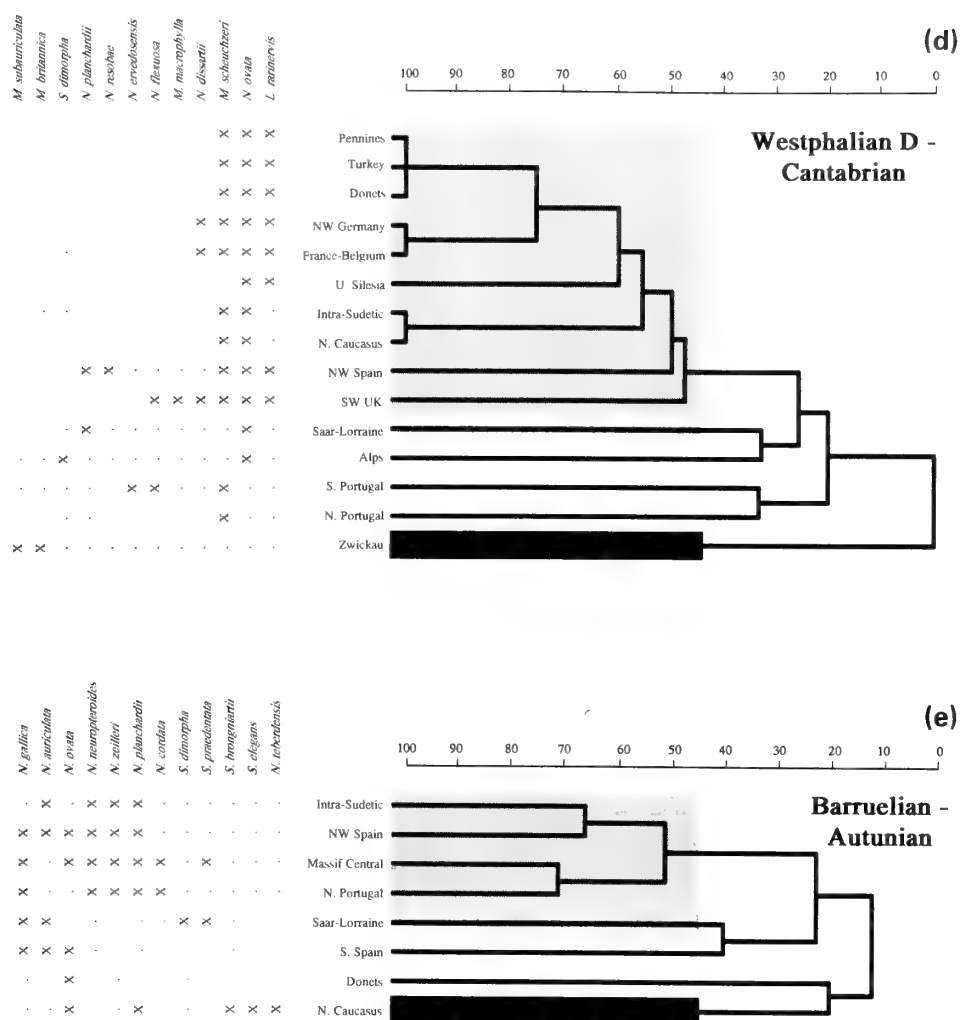
Fig. 25 *cont* (d) Westphalian D to Cantabrian; (e) Barruelian to Autunian.

studied, at least in recent years. There are some exceptions, such as Darrah's (1969) monograph on the Mazon Creek plant fossils, and some useful records by Gillespie *et al.* (1975), Gillespie & Pfefferkorn (1976), Gillespie & Crawford 1985) and Gillespie & Rheams (1985). These indeed suggest a close similarity to the European assemblages. However, on their own they are not really sufficient to allow a comprehensive assessment of the North American records, which is why they were not incorporated into the analysis presented in the present paper (for a further review of the North American records, see Pfefferkorn & Gillespie 1980).

The western part of North America in the Carboniferous has been assigned to two separate phytochoria, which may be referred to as the Cordillera Palaeoarea of the mid-west states and the Oregon Palaeoarea of the Pacific coastal area Pfefferkorn & Gillespie 1980, Cleal & Thomas *in* Cleal 991). No neuropteroids have been reported from the Oregon Palaeoarea. The Cordillera Palaeoarea is very poorly documented, with the sole exception of the plant fossils from the Manning Canyon Shale (Tidwell 1967). Of Tidwell's records, the most significant is of *Neuropteris* cf. *pocahontas* White, which is undoubtedly a neuralethopterid similar to *N. schlehanii*. However, his record of '*Neuropteris*' *gigantea* is undoubtedly incorrect (at least one pinnule in the figured specimen has a basiscopic lobe – it may in fact be an elongate neuralethopterid) and his '*Neuropteris*' *ampelina* Tidwell is a *Eusphenopteris*.

Gondwana. There are no neuropteroids recorded from the Carboniferous of the middle and high palaeolatitudes of Gondwana (the so-called pre-*Glossopteris* and early *Glossopteris* floras – reviewed by Wagner *et al.* 1985). However, the palaeoequatorial parts of Gondwana, such as the Mérida Andes of Venezuela, the Djerada Basin of Morocco and the Sud-Oronais region of Algeria, yield typical Euramerian-type assemblages. The published records include species of *Neuropteris*, *Laveineopteris*, *Macroneuropteris*, *Paripteris* and *Neurocallipteris* (Jongmans & Deleau 1951, Jongmans 1952b,

Pfefferkorn 1977, Migier 1982). However, these are either unillustrated records, or just show small fragments, which are difficult to assess; their generic affinities are probably correct, but any further statement will have to await a more complete documentation.

Cathaysia. Although in very similar palaeolatitudes to Europe during the Carboniferous, only a few neuropteroids are found in China. The most significant from an evolutionary point of view is *Paripteris*, which seems to have first evolved in China in the late Visean (possibly Brigantian) and only later migrated west to Europe in the Namurian (Laveine *et al.* 1989, 1992). The Chinese specimens have traditionally been referred to as *Paripteris gigantea* (e.g. Li *et al.* 1974, Yang *et al. in* Wagner *et al.* 1983). However, recent work by Zhang *et al.* (1992) and Laveine *et al.* (1992) has shown that, although similar, the Chinese material is not conspecific with that from Europe and it awaits a new name.

There is also some evidence that *Neuropteris* may occur in China. There are numerous records from the Upper Carboniferous (thought to be approximately equivalent to the Stephanian in the Heerlen Classification) of North China of *Neuropteris ovata*. However, their veining is denser and the pinnules more broadly attached to the rachis than the typical Westphalian D specimens of this species from Europe, and Gothan & Sze (1933) referred them to a separate species, *N. pseudovata*. Wagner (1963) went further, to suggest that there is a close similarity between these Chinese fossils and the species which is now referred to as *Neurocallipteris neuropteroides*. This clearly raises a difficulty as to the status of the Chinese fossils, as there is no published evidence of their cuticles to prove whether they are neuropterid or neurocallipterid. In view of their relative high stratigraphical occurrence, these Chinese fossils are in clear need of revision.

Li *et al.* (1974) described some fragmentary specimens from the Namurian of China as *Lopinopteris intercalata* Sze. Laveine *et al.* (1987) have argued that they may be very closely related to *Neuropteris obliqua*. However, there will have to be a more complete documentation of the Chinese material before its taxonomic position can be confirmed.

Angara. There have been a number of records of *Neuropteris* from this palaeokingdom (e.g. Neuburg 1948, Gorelova *et al.* 1973). Among the more completely known species are '*N.*' *pulchra* Neuburg and '*N.*' *izylensis* (Chirkova) Neuburg. Although only a few specimens of these species have been documented in the literature, and the illustrations of these are mostly poor, they demonstrate certain significant features of frond architecture: they have ultimate pinnae terminated by a pair of pinnules and intercalated pinnules on the penultimate racheis. These are characteristic features of the form-genus *Paripteris*, although the pinnule form and venation is rather different from any of the European or Chinese species. Also of possible paripterid affinity is '*N.* ' *dichotoma* Neuburg, although this observation is based on the similarity of its pinnules and venation to the European species *P. gigantea*; little of its frond architecture has been documented.

Two species with very large pinnules (up to 70 mm long) have been described under the names '*N.*' *siberiana* Zalessky and '*N.*' *balachonskiensis* Gorelova. One specimen of the former, figured by Neuburg (1948: pl. 31, fig. 1), shows pinnules apparently with two basal lobes or incipient pinnules (again, the quality of the illustrations make their interpretation difficult). A comparison with *Macroneuropteris* is thus

hinted at, but far more material needs to be examined before this could be confirmed.

A rather unusual-looking species has been described as '*N.*' *ignotus* Gorelova *in* Gorelova *et al.* (1973). It has very tapered, subfalcate pinnules, spaced widely along a very wide rachis, and is quite different from anything that has been previously assigned to the neuropteroid group. A comparison with the once-pinnate peltasperm frond *Compsopteris* is possible, although without more complete material, preferably including cuticles, this affinity would be difficult to confirm.

Most of the other Angaran species that have been assigned to *Neuropteris* (e.g. '*N.*' *tomiensis* (Zalessky) Radchenko, '*N.*' *orientalis* Radchenko) are all too small and poorly illustrated to assess. As far as it is possible to make out, other than some possible paripterids, no good examples of neuropteroid fronds have been described from these floras.

Kazakhstan. The Carboniferous plant assemblages found here are intermediate in composition between those typical of Eurameria and Angara (Meyen 1987). According to both Vakhrameev *et al.* (1978) and Cleal & Thomas *in* Cleal (1991), about half of both species and form-genera in the Middle Carboniferous (in the Russian chronostratigraphy, equivalent approximately to the Namurian and Westphalian of the Heerlen Classification) of Kazakhstan are also found in Europe, and include some neuropteroids.

The best documented records of Carboniferous plant fossils from here are by Radchenko (1954, 1985) and Oshurkova (1967). Other than some large, isolated pinnules from the Upper Carboniferous (in the Russian sense, i.e. approximately Stephanian), identified as the Angaran species '*Neuropteris*' *dichotoma* Neuburg (see above), most neuropteroid-like material originates from the upper Visean and Namurian. The latter are all characterized by relatively small, vaulted, lateral pinnules with a weakly developed midvein, and a distinctive, round apical pinnule. The lateral pinnules vary to an extent in shape, from round to oval to subrectangular with a round apex, and have been assigned to various species including *Neuropteris antecedens* Radchenko *non* Stur, *N. heterophylla* Oshurkova *non* Brongniart, *N. pseudoheterophylla* Radchenko, *N. bulupalganensis* Radchenko *non* Zalessky and *N. karagandensis* Borsuk. However, these morphological variants are frequently found associated together, and they almost certainly belong to one and the same species. Goganova *et al.* (1992) have recently described some remarkably complete examples of this species and found that it is fundamentally different from *Neuropteris*. They propose that the correct name is *Cardioneuropteris asiatica* (Radchenko) Goganova *et al.* Although the fronds are bipartite, producing tripinnate primary rachis branches, there are no intercalated elements between the secondary pinnae. Also, in close association were numerous *Aulacotheca*-like sporangial clusters, which in Europe are normally associated with the frond form-genus *Alethopteris*. It is clear that *Cardioneuropteris* is fundamentally different from any of the neuropteroid form-genera found in Europe.

Mention should be made of specimens recorded by Oshurkova (1967) from somewhat higher (probably Westphalian equivalent) strata under the name *Neuropteris obliqua*. Unfortunately, only one extremely small fragment was illustrated (Ibid.: pl. 15 fig. 8), which is totally inadequate for taxonomic assessment.

It seems that, other than the possible paripterid '*N.*'

dichotoma and the inadequately documented *N. obliqua*, no unequivocal neuropteroid form-genera (at least in the European sense) have been recorded from Kazakhstan.

CONCLUDING REMARKS

We are minded at the end of our study to quote from the preface to John Woodward's (1729) pioneering palaeontological study; *Now, that I have been for some time engaged in Mineral Studyes, with no small Application, 'tis a Pleasure to me to find that it has not been wholly without Fruit.* When we first started out on our project we intended it purely as a means of testing the robustness of the taxonomic scheme proposed by Cleal *et al.* (1990). However, we have ended up on a much longer journey into the realms of palaeogeography, biostratigraphy, palaeoclimatology and population dynamics. Trying to improve the taxonomy of a group of organisms, whether living or extinct, has its own internal logic, but we discovered that is has also provided an improved tool for understanding the pattern of the temporal and spacial distributions of the species. The distributions of the individual species were of course mostly already known, but the more general patterns were obscured by the wholly artificial generic taxonomy traditionally employed. Grouping the species into what seem to be more natural form-genera provided a context for at last seeing more clearly these more general patterns; we have been able to see the trees for the wood!

This demonstration of its geological utility of course also adds further support for the essential 'naturalness' of the revised taxonomic scheme. That a group of species responds in the same way to environmental pressures does not prove that they are closely related. However, if the species are also morphologically very similar at both the macroscopic (frond architecture) and microscopic (cuticles) levels, there must clearly be a strong likelihood that they are a genetically homogeneous group. There will always be the potential for convergent evolution to confuse the issue, especially with organs such as leaves, but by using as many morphological characters as possible it should be possible to detect this. A case in point is the close gross-morphological similarity between the mainly Westphalian D to Barruelian *Neuropteris ovata* and the mainly Stephanian C to Autunian *Neurocallipteris neuropteroides*. Some authors have gone as far as to suggest that the latter is a descendant of the former (e.g. Wagner 1963). However, their epidermal structures are very different, as are their apparent responses to environmental changes within the forests, and it is almost certain that the similarity in gross morphology merely represents convergent evolution.

Our study provides clear evidence of the long-known but often forgotten fact, that there is a close symbiotic relationship between the study of plant fossils and geology; the fossils cannot be properly understood without an understanding of the geological (sedimentological, stratigraphical, palaeogeographical) context in which they are found. Equally, the plant fossils provide invaluable palaeoecological, biostratigraphical and palaeophytogeographical data for improving our understanding of the geology. This information can then be re-cycled back to improve our understanding of the original vegetation (Cleal 1991: 223). As our study has demonstrated, this iterative process is dependent on the availability of a robust taxonomy, not only at the rank of species but also of form-genus. Obviously, a form-genus cannot be the exact equivalent of a whole-plant genus, being based only on a single plant organ. Nevertheless, the aim should be to make a form-genus as near as possible to a phylogenetically coherent concept (Cleal 1986), and this can only be achieved by detailed morphological and taxonomic study of the fossils.

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INDEX OF GENERA AND SPECIES

This is an index of the systematic section, not the whole paper. Species which are regarded as 'good' in the sense used in this paper are shown in bold Roman type, while earlier synonyms and combinations, and species based on inadequate type specimens, are in italics. The archaic spelling variant *Nevropteris* is not distinguished in the index, and its entries are to be found under *Neuropteris*.

The Upper Cretaceous ammonite *Pseudaspidoceras* Hyatt, 1903, in north-eastern Nigeria

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CONTENTS

SYNOPSIS. The following species of *Pseudaspidoceras* Hyatt occur in north-eastern Nigeria, from oldest to youngest: *P. pseudonodosoides* (Choffat), *P. footeanum* (Stoliczka), *P. paganum* Reyment and *P. flexuosum* Powell. *P. pseudonodosoides* is represented by paedomorphic populations. *P. flexuosum* marks the basal Turonian of the region. The remaining species are all of Late Cenomanian age. *P. pseudonodosoides* occurs in beds correlatable with the *Neocardioceras juddii* Zone in south-western New Mexico but the Nigerian sequence is expanded in comparison; no equivalents of the horizons with *P. footeanum* and *P.paganum* are known in the former region. The Nigerian material demonstrates the great potential of *Pseudaspidoceras* in detailed correlation over the Cenomanian-Turonian boundary. Below the beds with *Pseudaspidoceras*, specimens probably referrable to *Burroceras* Cobban, Hook & Kennedy occur.

INTRODUCTION

In recent years renewed attention has been paid to the Cenomanian-Turonian ammonite faunas of north-eastern Nigeria (Wozny & Kogbe 1983, Popoff *et al*. 1986, Meister 1989, Zaborski 1990, Courville *et al*. 1991, Courville, 1992). Early descriptions were provided by Woods (1911), Reyment (1954*a*, 1954*b*, 1955) and, especially, Barber (1957, 1960), but these works generally lacked information concerning the precise stratigraphical occurrences of the material involved. The impetus for fresh studies has largely been provided by the opening of the Ashaka Cement Company's quarry some 100 km north of the town of Gombe. Here, unusually for the region, large ammonite collections can be made within a clear stratigraphical context. Coupled with information gathered from scattered localities elsewhere in north-eastern Nigeria, notably the Pindiga stream section, data from Ashaka have enabled a regional ammonite biostratigraphy to be worked out (Zaborski 1990). North-eastern Nigeria is emerging as a

region of key importance in understanding the ammonite succession across the Cenomanian-Turonian boundary. The expanded sequences are dominated by vascoceratid faunas, but also contain acanthoceratid ammonites of wider geographical distribution, allowing correlations to be made with zonal schemes from north-western Europe and North America. One of the genera having such value is *Pseudaspidoceras* Hyatt, 1903, which is represented by four species, in ascending stratigraphical order: *P. pseudonodosoides* (Choffat), *P. footeanum* (Stoliczka), *P. paganum* Reyment and *P. flexuosum* Powell. In addition, forms probably referrable to the closely related genus *Burroceras* Cobban, Hook & Kennedy, 1989 occur lower in the sequence. The purpose of this contribution is to document the Nigerian material and to highlight its stratigraphical value.

The Ashaka and Pindiga sections

Although *Pseudaspidoceras* occurs widely in north-eastern Nigeria, only at Ashaka and Pindiga have more than one

species been collected in an observed stratigraphical sequence. The locations of these sections and other localities mentioned herein were shown by Zaborski (1990), while a general account of the geology of the region was given by Carter *et al.* (1963).

A continuous section made up of ammonite-bearing limestones and interbedded barren shales of Late Cenomanian and Early Turonian age is exposed at Ashaka (Fig. 1). The Pindiga stream section is discontinuous and partly subject to burial and re-exposure during the summer rains. Figure 1 shows those parts of the section that have been logged over the period 1986 to 1992.

The Ashaka section is as follows (see Fig. 1; numbers in parentheses are the equivalent horizons in Meister (1989):

Bed		Metres
	Alternating shales and sandstones, the latter glauconitic, feldspathic and calcite-cemented below, quartzose above and with a 15 cm shelly, sandy limestone towards the top	12·00
	Glauconitic, gypsum-bearing clay	0·10
X (34)	Pale grey, nodular limestone with clay and gypsum laminae. *Vascoceras harttii* (Hyatt), *V. obscurum* Barber, *Pseudotissotia nigeriensis* (Woods), *Eotissotia simplex* Barber	0·43
	Blue-grey shales with gypsum	0·27
W (34)	Yellow, nodular limestone with *Thalassinoides* burrows on upper surface. *Pseudotissotia nigeriensis*, *Eotissotia simplex*	0·08
	Blue-grey shales with gypsum	0·25
V (34)	Yellow, nodular limestone with gypsum. *Thalassinoides* burrows on upper surface. *Pseudotissotia nigeriensis*, *Eotissotia simplex*, *Wrightoceras munieri* (Pervinquière)	0·06
	Blue-grey shales with gypsum	2·45
U (32)	Greenish-grey nodular limestone, weathering to creamy yellow, with clay and gypsum stringers. *Vascoceras* sp., *Pseudotissotia nigeriensis*, *Eotissotia simplex*	0·30
	Blue-grey shales with gypsum	1·55
T2 (30)	Glauconitic, calcareous clay with black phosphate pebbles. *Pseudaspidoceras flexuosum* Powell, *Watinoceras* aff. *coloradoense* (Henderson), *Vascoceras proprium proprium* (Reyment), *V. obscurum* Barber, *Thomasites gongilensis* (Woods), *Pseudotissotia nigeriensis*, *Wrightoceras munieri* and *Choffaticeras* sp.	0·06
T1 (30)	Cream-brown limestone with *Pseudotissotia nigeriensis* and *Vascoceras proprium proprium* (30)	0·12
	Blue-grey shales with gypsum	0·24
S (28)	Cream-brown calcareous concretions, forming a continuous layer in places	0·07
	Dark grey to blue-grey shales	1·00
	Glauconitic, calcareous clay	0·08

R (26)	Hard, pale grey limestone. *Pseudaspidoceras paganum* Reyment, *Vascoceras proprium globosum* (Reyment), *Thomasites gongilensis*, *Pseudotissotia nigeriensis*	0·26
	Calcareous, glauconitic, shelly clay, with shale partings forming a more distinct shale unit up to 50 cm thick in some places	0·10
Q (24)	Massive, hard, grey-green limestone. *Vascoceras* sp., *Thomasites gongilensis*	0·33
	Dark grey shales with gypsum; a 1–4 cm horizon crowded with small thin-shelled bivalves, bone fragments and small phosphatic pebbles occurs 15 cm below the top in some places	1·40
P	Clay, with gypsum and scattered white calcareous nodules	0·03
	Dark grey shales with gypsum	1·40
O (21–22)	Hard, grey-green, nodular limestone in top 8–15 cm, rubbly limestone with shale partings below. *Pseudaspidoceras footeanum* (Stoliczka), *Vascoceras proprium costatum* (Reyment), *V. proprium globosum*, *V. bullatum* (Schneegans), *V. nigeriense* Woods, *V. cauvini* Chudeau, *Thomasites gongilensis*, ammonite gen. et sp. nov.	0·32
N (20)	Hard, grey, massive crystalline limestone	0·50
M (19)	Rubbly, impure limestone with shale partings. *Pseudaspidoceras pseudonodosoides* (Choffat), *Vascoceras* sp. nov. aff. *gamai* Choffat, *V. cauvini*	0·73
L (18)	Hard, pale cream-grey, massive limestone	0·45
K (17)	Rubbly, impure limestone with shale partings. *Pseudaspidoceras pseudonodosoides*, *Vascoceras* sp. nov. aff. *gamai*, *V. cauvini*	0·50
J (16)	Hard, grey limestone, cross-bedded in places	0·42
I (14–15)	Hard, grey limestone, cross-bedded in places	1·07
H (12–13)	Hard, grey limestone, cross-bedded in places. *Vascoceras cauvini*	0·85
G (11)	Massive, pale to dark grey limestone, passing laterally into bioturbated grey-green limestone. *Vascoceras cauvini*	0·80
F (10)	Rubbly limestone with interbedded harder limestones. *Burroceras?* sp., *Vascoceras cauvini*	0·70
E (10)	Rubbly, grey-green to dark grey limestone with clay and gypsum stringers. *Vascoceras cauvini* in upper part	1·20
D	Massive, grey-green, glauconitic, quartzose limestone. *Exogyra*-rich. *Nigericeras gadeni* (Chudeau)	0·90
C	Brown-yellow, calcareous sandstone	0·20
B	Ferruginous sandstone	0·09
A	Grey-green, fine-grained, poorly consolidated sandstone becoming calcareous in its upper part	2·00

The Pindiga section, or more precisely that part of it which has been seen, is as follows, from top to bottom, see Fig. 1 (numbers in parentheses are the equivalent horizons in Popoff *et al.* (1986)):

Bed		Metres
	Blue-grey shales with gypsum (base of Pindiga Formation shale member)	
V (22)	Earthy, yellow-brown, glauconitic, calcareous clay, with gypsum and white calcareous nodules. *Pseudotissotia nigeriensis, Eotissotia simplex*	0·15
	Blue-grey shales with gypsum	1·00
U (21)	Pale grey-green, poorly bedded, impure limestone. *Pseudotissotia nigeriensis, Eotissotia simplex*	0·70
T (21)	Brown-grey, poorly bedded, calcareous shale, with gypsum and shale laminae. *Pseudotissotia nigeriensis, Eotissotia simplex*	0·27
	Blue-grey shales with gypsum	0·15
S (21)	Cream-grey, irregularly bedded marl. *Pseudotissotia nigeriensis, Eotissotia simplex*	0·38
R (17)	Light grey, poorly bedded limestone with shale partings. *Pseudotissotia nigeriensis*. 7 cm hard, pale grey, nodular limestone capping	0·40
Q	Pale yellow, nodular limestone	0·06
	Blue-grey shales	0·04
	Hard, fine-grained grey limestone	0·08
P	Porous grey limestone. *Thomasites gongilensis, Pseudotissotia nigeriensis*	0·61
	Limestone, rubbly	0·12
	Hard, fine-grained grey limestone	0·08
	Blue-grey shales	2·10
O	Intensely hard, grey, orange-weathering, shelly limestone. ?*Pseudaspidoceras paganum, Vascoceras proprium globosum, Thomasites gongilensis, Pseudotissotia nigeriensis*	0·22
N (7)	Hard, grey, laminated limestone with *Thalassinoides* burrows on upper surface. *Pseudaspidoceras pseudonodosoides, Vascoceras* sp. nov. aff. *gamai, V. cauvini*	0·18
	Gypsum band	0·02
	Blue-grey shales with gypsum	0·10
M (7)	Decalcified white limestone with *Pseudaspidoceras pseudonodosoides, Vascoceras* sp. nov. aff. *gamai* and ammonite gen. et sp. nov. preserved in a white clay matrix up to	0·05
	Blue-grey shales with gypsum	0·35
	Gypsum band	0·02
L (7)	Marly limestone. *Vascoceras* sp. nov. aff. *gamai*	0·08
	Gypsum band	0·02
	Blue-grey shales	0·90
K (5,6)	Hard, grey, nodular limestone	0·15
	Blue-grey shales	0·10
(5,6)	Hard, grey, shelly limestone. Reworked *Vascoceras cauvini* on upper surface	0·26

I (4)	Roughly bedded, hard, grey, nodular limestone with numerous *Hemiaster*	0·45
H (4)	Intensely burrowed, pale grey marl with numerous *Hemiaster. Burroceras?* sp., *Vascoceras cauvini*	0·23
G (4)	Roughly bedded, impure limestone. *Vascoceras cauvini*	0·17
	Blue-grey shales	0·06
F (4)	Bryozoan biostrome in lower part, passing upwards into 75 cm thick *Plicatula* biostrome, with *Plicatula* becoming less common upwards	1·21
	Blue-grey shales	1·00
E	Massive, hard, pale grey limestone	0·13
	Blue-grey shales	0·50
D	Shelly, marly limestone with 1 cm shale parting in the middle	0·07
	Blue-grey shales	0·30
C	Impure limestone	0·06
	Blue-grey shales	0·20
B	Impure limestone	0·10
A (2)	Rough-bedded, grey limestone with phosphatic particles at the base. Numerous *Exogyra*; *Metengonoceras dumbli* (Cragin), *Placenticeras (Karamaites) cumminsi* (Cragin), *Nigericeras gadeni*	0·42

Unit A at Pindiga is the '*Exogyra* Limestone' of Barber (1957). Units F–I are his 'Echinoid Limestone' while units O and P are his '*Gombeoceras* Limestones 1 and 2'.

SYSTEMATIC DESCRIPTIONS

Repositories. Unless otherwise stated all the material referred to herein is in the Department of Palaeontology, The Natural History Museum, London. Only these specimens are individually identified though many additional examples of *Pseudaspidoceras pseudonodosoides* and *P. flexuosum* from Ashaka have also been studied.

Superfamily **ACANTHOCERATACEAE** Grossouvre, 1894
Family **ACANTHOCERATIDAE** Grossouvre, 1894
Subfamily **EUOMPHALOCERATINAE** Cooper, 1978
Genus *PSEUDASPIDOCERAS* Hyatt, 1903
(=*Ampakabites* Collignon, 1965a)

TYPE SPECIES. *Ammonites footeanus* Stoliczka, 1864; by original designation.

REMARKS. Proposed by Hyatt (1903: 106), the genus *Pseudaspidoceras* has subsequently been discussed by Pervinquière (1907), Freund & Raab (1969), Matsumoto (*in* Matsumoto, Kawashita, Fujishima & Miyauchi 1978), Wright & Kennedy (1981), Kennedy *et al.* (1987) and Cobban *et al.* (1989). It includes evolute ammonites with square to rectangular whorl sections. There are distant to rather dense, rounded to sharp, and rectiradiate to curved ribs in the middle whorls. Umbilical, inner and outer ventrolateral tubercles are present. Intercalated ribs frequently occur. Freund & Raab (1969: 13) considered a wide lateral lobe to be characteristic of the suture in *Pseudaspidoceras*. Matsumoto (1978) pointed out that *Mammites wingi* Morrow, 1935
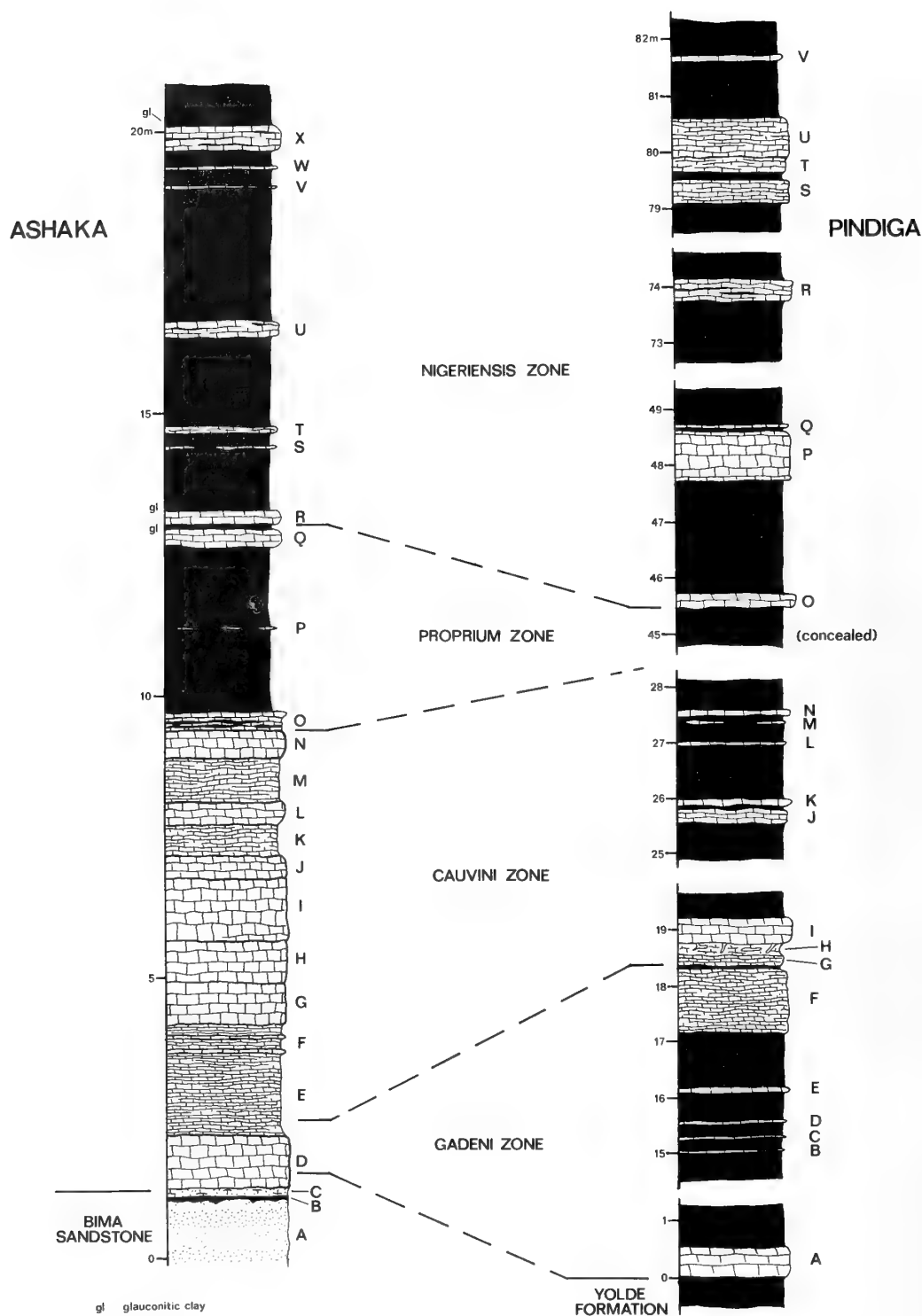
Fig. 1 Stratigraphical sections in the Pindiga Formation exposed at Ashaka Quarry and in the Pindiga stream.

and *M. dixeyi* Reyment, 1955 share this feature but these relatively involute and stout forms have since been included by Cobban & Hook (1983a) in their new genus *Morrowites*.

Hyatt (1903) assigned *Pseudaspidoceras* to the subfamily Mantelliceratinae. Most subsequent workers have included the genus in the Mammitinae (see, for example, Pervinquière 1907, Reyment 1955, Wright 1957, Barber 1957, Matsumoto 1978, Wright & Kennedy 1981). Descriptions of the inner whorls of *P. flexuosum* by Kennedy *et al.* (1987) and of *P. pseudonodosoides* by Cobban *et al.* (1989), however, revealed multiplication of the outer ventrolateral tubercles and the presence of constrictions, demonstrating a close relationship with *Euomphaloceras* Spath, 1923. *Pseudaspidoceras* is therefore best referred to the Euomphaloceratinae Cooper. The type species of *Ampakabites* Collignon, *Kamerunoceras (Ampakabites) auriculatum* Collignon (1965a: 29, pl. 388, fig. 1662; pl. 389, fig. 1664), was regarded as a synonym of *P. flexuosum* by Kennedy *et al.* (1987). Collignon (*in* Cobban & Scott 1972: 81) had, himself, earlier indicated that *Ampakabites* was better treated as a subgenus of *Pseudaspidoceras* rather than *Kamerunoceras*.

Pseudaspidoceras has a stratigraphical range from Upper Cenomanian to Lower Turonian. It occurs in Texas, New Mexico, Arizona, Colorado, Mexico, Brazil, Germany, southern England, Portugal, Tunisia, Egypt and the Middle East, Algeria, Angola, Niger, Nigeria, Madagascar, southern India and (?)Japan.

Pseudaspidoceras pseudonodosoides (Choffat, 1898)

Figs 2–5, 8, 14

1898 *Acanthoceras*(?) *pseudonodosoides* Choffat: 65, pl. 16, figs 5–8; pl. 22, figs 32, 33.
1925 *Mammites pseudonodosoides* (Choffat) Diener: 175.
1957 *Pseudaspidoceras* sp. Barber: 11, pl. 25, fig. 8.
1969 *Pseudaspidoceras* cf. *P. pseudonodosoides* (Choffat); Freund & Raab: 14, pl. 1, figs 10, 11; text-figs 4j–k.
1989 *Pseudaspidoceras pseudonodosoides* (Choffat); Meister: 6, pl. 2, fig. 1; text-fig. 2.
?1989 *Pseudaspidoceras* sp. Luger & Gröschke: 372, text-fig. 6I.
1989 *Pseudaspidoceras pseudonodosoides* (Choffat); Cobban, Hook & Kennedy: 40, figs 41, 81–83 (with synonymy).
1990 *Pseudaspidoceras* cf. *pseudonodosoides* (Choffat); Zaborski: figs 22a, b.

MATERIAL AND OCCURRENCE. Twelve specimens, C.93333, C.93335, C.93353–4, C.93573–5, C.93982 from the Pindiga

Table 1 Morphometric data for *Pseudaspidoceras pseudonodosoides* (Choffat, 1898).

	D	Wb	Wh	U
C.47620	92	36 (39)	34 (27)	36 (39)
C.91232	91	40 (44)	36 (39.6)	29 (32)
C.93574	87	–	31 (35.6)	35 (40)
C.93335	65	34 (52)	25 (38.5)	–
C.93757	58	31 (53.5)	22 (38)	20 (34.5)

Dimensions (in mm). D, diameter; Wb, whorl breadth; Wh, whorl height; U, umbilical diameter. Figures in parentheses are dimensions as a percentage of the total diameter.

Formation, unit M, Ashaka; C.91232 from the lower part of the Dukul Formation at Dukul (see Zaborski 1990: fig. 28); C.93594 from the Pindiga Formation, unit M, Pindiga; C.93756–7, from the Pindiga Formation, Deba Habe. In addition a single specimen from the Pindiga Formation, Bularaba (C.47620, see Barber 1957: 11) has been studied. The species is very abundant in unit M at Ashaka and also occurs in some numbers in unit K there. It occurs as a rarity in units M and N at Pindiga. The Deba Habe specimens come from a 10 cm limestone occurring less than 1 m below the level at which *Vascoceras proprium costatum* and *V. nigeriense* appear. No precise stratigraphical data are available for the Bularaba specimen.

DESCRIPTION. Most individuals have a maximum adult diameter of 90–100 mm though some reach 120 mm. Whorl breadth is slightly to distinctly greater than whorl height.

Only in C.47620 and C.93757 (Figs 5, 8) is the ornament of the septate whorls well displayed. At a diameter of 6 mm in C.93757 there are six prominent lateral bullae in the last half whorl. They pass over the ventrolateral shoulders and merge with bullate outer ventrolateral tubercles. Isolated outer ventrolateral tubercles may be intercalated. In the last preserved whorl, up to a diameter of 58 mm, there are 9 umbilical tubercles. At first they are rounded and give rise to robust, rounded, rectiradiate ribs on the low flanks. The ribs bear a rounded inner ventrolateral tubercle but weaken as they pass over the venter where they may branch or be slightly convex. There are weak outer ventrolateral tubercles but they disappear at a diameter of 35 mm. Intercalated ventral ribs also occur; they may be as pronounced as the main ribs or take the form of fine, convex riblets. The latter type are more persistent, being present up to diameters of at least 50 mm. At diameters in excess of 45 mm the inner ventrolateral tubercles weaken, then disappear. The umbilical tubercles persist but become highly bullate and give rise to broad, rounded ribs on the inner flank region.

In C.47620 (Fig. 5) there are 13 broad, rounded, rectiradiate ribs in the whorl up to a diameter of 40 mm. Nearly all arise at prominent umbilical bullae. They weaken in the mid-flank region before bearing prominent, rounded inner ventrolateral tubercles. The latter structures have disappeared by a diameter of 45 mm. There are no outer ventrolateral tubercles at this stage. Though the earlier part of the venter in this restored specimen is concealed, Barber (1957: 11) mentioned the presence of such tubercles on the early whorls. Umbilical bullae persist onto the adult body chamber where they become weaker, elongate structures giving rise to irregularly developed, usually weak, concave ribs on the flanks. The body chamber has a rounded outline in contrast to the more rectangular, depressed section of the septate whorls.

Umbilical bullae also persist onto the body chamber in C.91232 from Dukul (Fig. 4) but here there are no flank ribs. The material from Ashaka consists almost entirely of poorly preserved body chambers which are generally smooth and with a rounded whorl section. C.93335 (Fig. 3) and C.93982 are unusual in retaining a rather rectangular whorl section and ribbing on the body chamber. In C.93982 the ribs extend from umbilical bullae across the flanks and ventrolateral shoulders where they terminate. In C.93335, however, umbilical bullae are weakly developed but ventrolateral swellings which give rise to rib-like structures on the inner part of the flank are present. C.93574 (Fig. 2) shows broad,
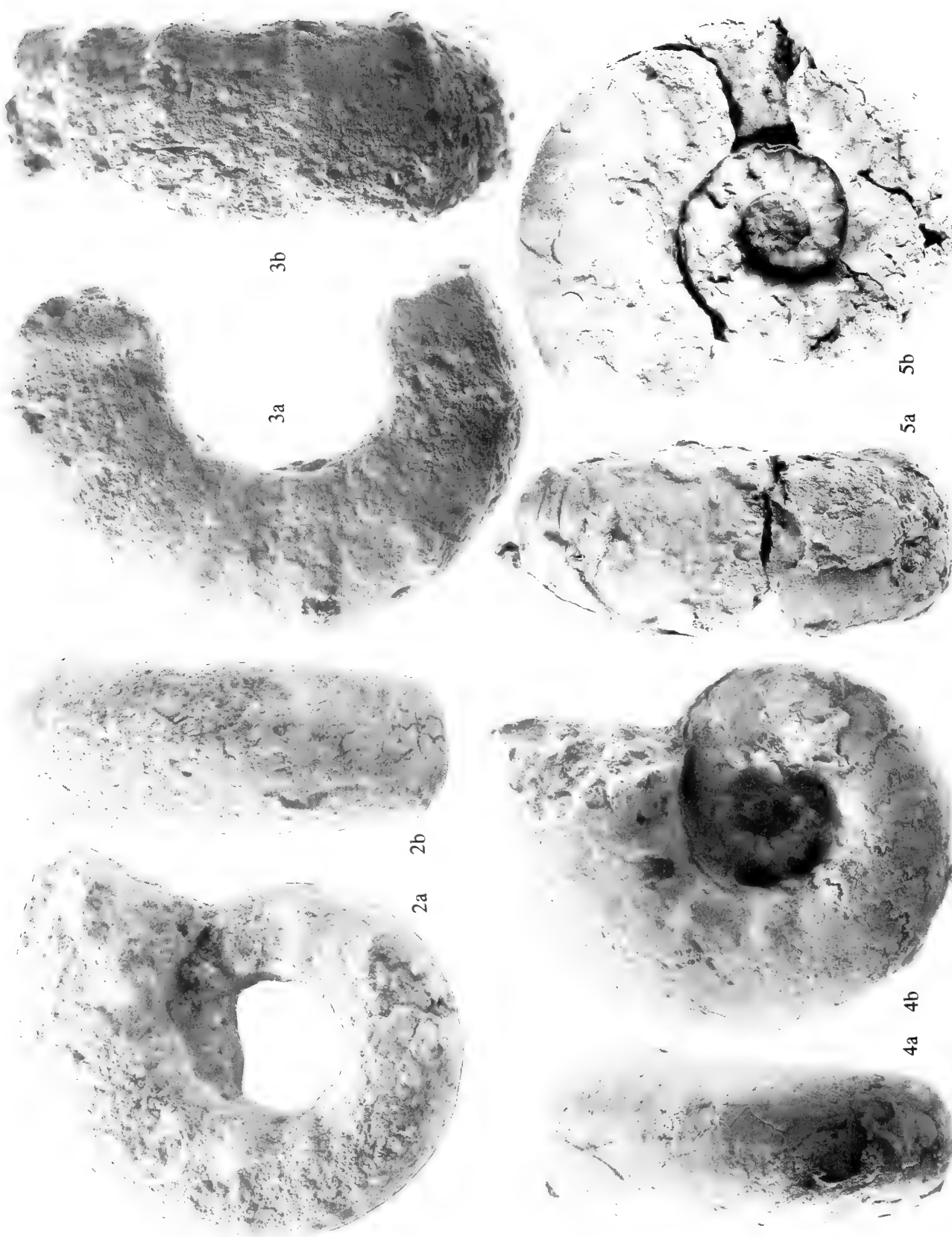
Figs 2–5 *Pseudaspidoceras pseudonodosoides* (Choffat). Figs 2, 3, Pindiga Formation, unit M, Ashaka. Fig. 2a, b, C.93574, x1. Fig. 3a, b, C.93335, x1. Fig. 4a, b, Dukul Formation, Dukul.

rectiradiate ribbing on the adoral part of the phragmocone but the body chamber is smooth. Certain specimens, for example that figured by Meister (1989: pl. 2, fig. 1) and C.93573, retain rather spinose ventrolateral tubercles on the body chamber.

Specimens seen in units M and N at Pindiga are all portions of the early whorls. One pathological specimen (C.93594, Fig. 14) has a diameter of some 50 mm and an ornament of umbilical bullae and abnormally developed inner ventrolateral tubercles, only one of the pair being present and displaced towards the siphonal line.

Sutures in the Nigerian material described above are relatively simple with rather short, uncomplicated elements. The lateral lobe is often unusually narrow for the genus. When it is broader it is subdivided by a short median element.

REMARKS. The lectotype of *P. pseudonodosoides* (selected by Cobban *et al.* 1989: 40) is the specimen figured by Choffat (1898: pl. 16, fig. 5). It is fully septate, has a diameter of about 90 mm, and is ornamented with strong umbilical tubercles, broad, rectiradiate ribs weakening in the mid-flank region, strong inner ventrolateral tubercles and, up to a diameter of about 60 mm, weaker outer ventrolateral tubercles. The whorls are distinctly broader than high and the venter is flattened to slightly concave. Choffat had only a few specimens at his disposal but recently Cobban *et al.* (1989) described a large collection from New Mexico which provides a wealth of information, especially regarding intraspecific variation. These forms have whorls slightly to distinctly broader than high, the flanks being flat and the venters flattened to broadly rounded. Ribs are generally rounded but may be sharp and narrow. There are 3–7 umbilical tubercles, 4–12 inner ventrolateral tubercles and 7–12 outer ventrolateral tubercles in each half whorl. Ribbing is generally best developed on the inner septate whorls while the outer ventrolateral tubercles weaken and disappear at diameters of 60–70 mm. Where they persist they may be expanded into oblique, rib-like structures. There is a great range of adult sizes but no evidence of size dimorphism; the diameter at the base of the body chamber varies from 61–182 mm, while overall maximum sizes are up to 300 mm.

The Nigerian collection conforms well with the lectotype, and, in ornament and general shell proportions, with the more coarsely decorated material from New Mexico. Although some of the latter specimens may have a comparable adult diameter, the material from north-eastern Nigeria, without regard to its exact locality, has a consistently smaller adult size of 90–120 mm. Material from Israel, referred to *P.* cf. *P. pseudonodosoides* by Freund & Raab (1969: 14–15), also includes forms reaching a diameter of over 300 mm, though some show whorls higher than broad and persistent outer ventrolateral tubercles and may be better included elsewhere. Meister (1989: 9) suggested that *P. paganum* (see below), a stratigraphically higher species, was hypermorphic in comparison to *P. pseudonodosoides*. More precisely, however, the north-eastern Nigerian poulations of the latter species are probably paedomorphic. There is no evidence of size dimorphism in this material, a similar adult size is found in all the individuals from Ashaka, Dukul and Bularaba. In this regard it is of interest to note the association of *P. pseudonodosoides* with large numbers of *Vascoceras* sp. nov. aff. *gamai* (=*Vascoceras* sp. juv. of Barber 1957: 27, pl. 5, figs 2, 4, 7; pl. 27, figs 10–15; *Plesiovascoceras* aff. gr. *homi* (Reeside) of Meister 1989: 11, pl. 4, figs 2, 3, 5;

Paravascoceras gr. *evolutum* (Schneegans) of Meister 1989: 14, pl. 5, fig. 4; text-fig. 10) at Ashaka, Pindiga and Deba Habe. This *Vascoceras* has an adult body chamber homeomorphic with and of comparable size (about 100 mm) to that in most of the co-occurring *P. pseudonodosoides*. The flank ribbing in the early whorls of the former may also resemble that in *P. pseudonodosoides*. The two are difficult to distinguish on the basis of poorly preserved material. The simplified suture in these *P. pseudonodosoides* even sometimes approaches that in *Vascoceras*. Size and form of *P. pseudonodosoides* in north-eastern Nigeria may have been under strong environmental control.

Pseudaspidoceras tassaraense Meister *et al.* (1992: 67, pl. 9, figs 2, 4, 7; pl. 10, figs 1, 2; text-fig. 12) from Niger is also adult at a diameter of only some 100 mm and loses its ornamentation early to develop a rounded whorl section. Meister *et al.* (1992) included the *Pseudaspidoceras* sp. of Barber (1957: 11, pl. 25, fig. 8), here considered as *P. pseudonodosoides*, in synonymy. *P. tassaraense* is closely similar to the present material and is probably conspecific.

P. tassaraense is known only from the Monts Iguellala region. Its precise stratigraphical level is difficult to determine in respect of other faunas in Niger. It occurs above *Nigericeras gadeni* and *Cibolaites*? *africaensis* Meister *et al.* (1992), the latter being unknown in Nigeria. Meister *et al.* (1992) inferred a position equivalent to a level between units R and T at Ashaka for *P. tassaraense*, that is, well above the horizons with *P. pseudonodosoides* there (units K and M). Occurring alongside *P. tassaraense* in Niger are *Nigericeras jacqueti involutum* Meister *et al.* (1992: 68, pl. 4, figs 3–5; text-fig. 14) and *Vascoceras* aff. gr. *silvanense* Choffat (Meister *et al.* 1992: 78, pl. 8, fig. 6; text-fig. 18). The *V. cauvini* which accompany *P. pseudonodosoides* in Nigeria may resemble *N. jacqueti involutum* in degree of compression and lack of juvenile ornament but are consistently more evolute. The inner whorls of certain *Vascoceras* occurring at the same levels, however, are similar to the *V.* aff. gr. *silvanense* of Meister *et al.* (1992) (see Zaborski 1991; fig. 18).

If *P. tassaraense* is conspecific with the present material then its stratigraphical level is almost certainly lower than that suggested by Meister *et al.* (1992). It would occur between their Gadeni and Cauvini zones, that is equivalent to their Pseudonodosoides to Evolutum zones in north-eastern Nigeria (Meister *et al.* 1992: figs 22–26).

Pseudaspidoceras footeanum (Stoliczka, 1864)

Figs 6, 7, 9, 10

1864 *Ammonites footeanus* Stoliczka: 101, pl. 52, figs 1, 2.
1887 *Ammonites pedroanus* White: 217, pl. 22, figs 1, 2.
1915 *Mammites (Pseudaspidoceras) footeanus*(?) (Stoliczka); Greco: 208, pl. 17, fig. 5.
1936 *Pseudaspidoceras pedroanum* (White); Maury: 231, pl. 21, figs 1, 2.
1972 *Pseudaspidoceras pedroanum* (White); Reyment & Tait: pl. 3, fig. 12.
1978 *Pseudaspidoceras* aff. *pedroanum* (White); Chancellor, Reyment & Tait: 91, figs 8–10.
1982 *Pseudaspidoceras footeanum* (Stoliczka); Chancellor: 92, figs 2A, 24, 25.
1985 *Pseudaspidoceras footeanum* (Stoliczka); Howarth: 98, figs 30–33.
1987 *Pseudaspidoceras footeanum* (Stoliczka); Kennedy, Wright & Hancock: 38, text-fig. 4.
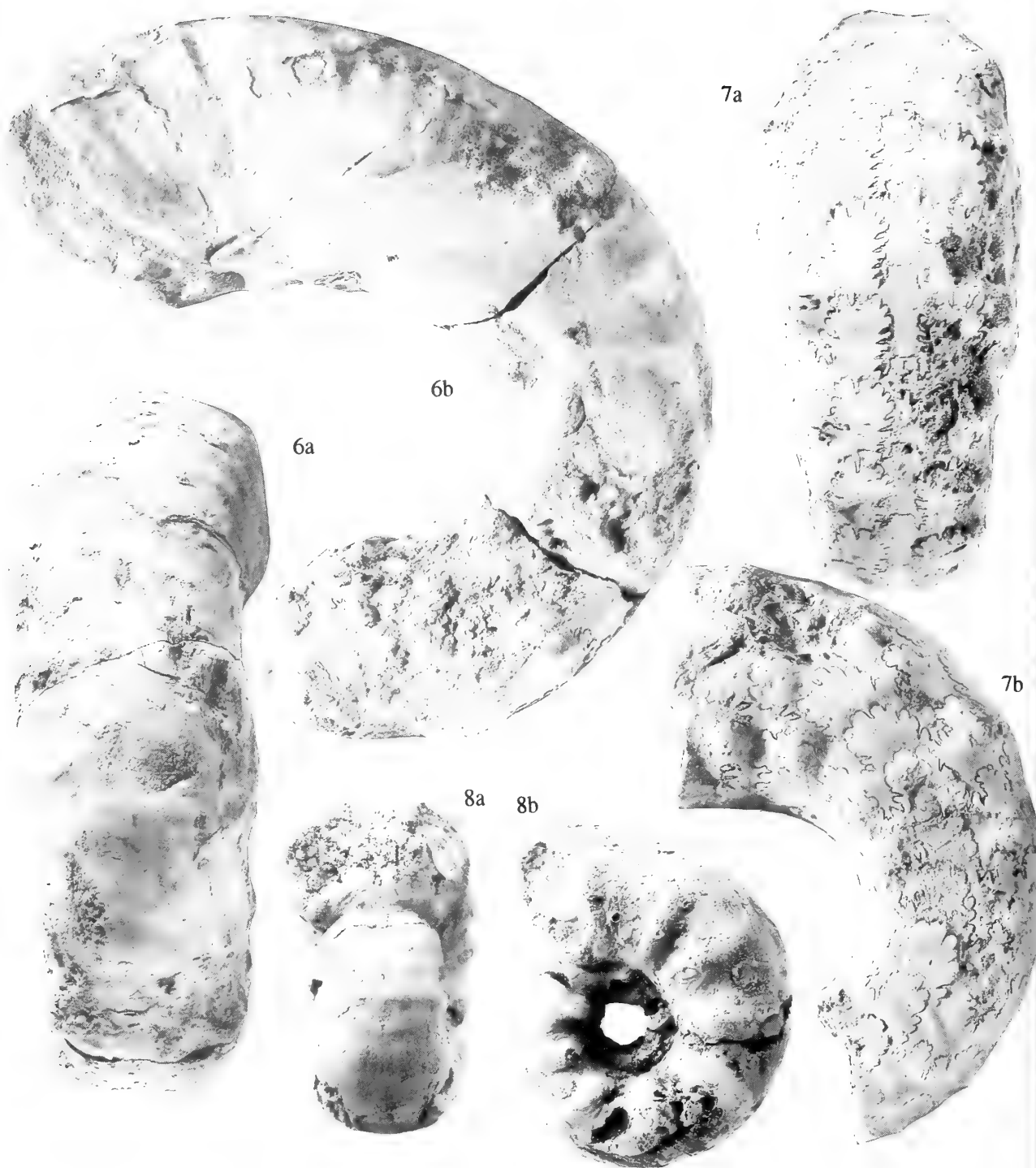
Figs 6, 7 *Pseudaspidoceras footeanum* (Stoliczka). Pindiga Formation, unit O, Ashaka. Fig. 6a, b, C.93577, x0.67. Fig. 7a, b, C.93576, x0.75. **Fig. 8a, b** *Pseudaspidoceras pseudonodosoides* (Choffat). Pindiga Formation, Deba Habe. C.93757, x1.

igs 9, 10 *Pseudaspidoceras footeanum* (Stoliczka). Fig. 9, Pindiga Formation, unit O, Ashaka. C.93578, x0.67. Fig. 10a, b, Pindiga
Formation, collected loose from the top of unit O, Ashaka. C.93362, x1. **Figs 11, 12** *Pseudaspidoceras flexuosum* Powell. Pindiga
Formation, unit T2, Ashaka. Fig. 11a, b, C.93560, x1. Fig. 12a–c, C.93567, x1.

1992 *Pseudaspidoceras* gr. *pseudonodosoides* (Choffat);
      Courville: pl. 1, fig. 2; pl. 2, fig. 1; pl. 3, figs 1,2

MATERIAL AND OCCURRENCE. Seven specimens, C.93309, C.93362, C.93576-8, C.93764, C.93927, all from the Pindiga Formation, unit O, Ashaka, except C.93362 which was collected loose from the top of this unit. The species occurs throughout unit O both in the rubbly limestone below and the hard, nodular capping horizon.

Table 2 Morphometric data for *Pseudaspidoceras footeanum* (Stoliczka, 1864).

	D	Wb	Wh	U
C.93577	210	70 (33)	67 (32)	–
C.93309	170	65 (38)	56 (33)	–
C.93576	135	58 (43)	55 (41)	–
C.93362	65	30 (46)	27·5 (42)	22 (34)

Dimensions (in mm). D, diameter; Wb, whorl breadth; Wh, whorl height; U, umbilical diameter. Figures in parentheses are dimensions as a percentage of the total diameter.

DESCRIPTION. An evolute form with whorls a little broader than high. The flanks are flattened and the venter flattened to broadly rounded on the phragmocone, but the adult body chamber may assume an evenly rounded outline. The maximum diameter attained is about 250 mm.

The earliest growth stages have not been seen. The smallest specimen available (C.93362, Fig. 10) has a diameter of 65 mm and consists of half of one of the middle septate whorls. The flanks are flattened, the ventrolateral shoulders sloping and the venter broadly rounded. There are three prominent and four feeble umbilical bullae giving off wide to narrow ribs which weaken in the mid-flank region before passing into prominent, rounded inner ventrolateral tubercles which are also of irregular strength. The ribs curve forwards and bifurcate over the ventrolateral shoulders before terminating in well developed conical to bullate outer ventrolateral tubercles which are often obliquely directed forwards. There may be one or two pairs of outer ventrolateral tubercles intercalated with those of the main ribs.

C.93576 (Fig. 7) has a diameter of 140 mm and consists of about half of one of the later septate whorls. There are eight umbilical bullae which give rise to low, broad, rounded, mostly radial ribs which so weaken as to virtually disappear in the mid-flank region. One of the ribs bifurcates with the adoral branch curved distinctly forwards. Most of the ribs bear prominent, rounded inner ventrolateral tubercles. Occasional intercalated inner ventrolateral tubercles are present. The ribs cross the ventrolateral shoulders and terminate at weaker outer ventrolateral tubercles situated close to the siphonal line. The latter tubercles vary from spinose to rounded to bullate in shape and are situated opposite to or slightly adoral of the inner ventrolateral tubercles. They become less spinose during growth.

C.93309 has a diameter of about 170 mm and consists of the adoral part of the near-adult phragmocone and the base of the body chamber. The whorl section is subrectangular, the flanks and the venter being flattened. Umbilical bullae give rise to broad, low, unevenly developed ribs, effaced in the mid-flank region and strengthening again as they cross the ventrolateral shoulders where they pass into massive, rounded inner ventrolateral tubercles, again of uneven strength. The ribs terminate at very broad, low, rounded to bullate outer ventrolateral tubercles.

Two adult body chambers are available. C.93577 (Fig. 6) has a diameter of some 210 mm. Ornament declines markedly and the whorl section becomes broadly and evenly rounded in this individual. Towards the aperture there are narrow, sharp ventrolateral ribs of uneven strength and spacing which are asymmetrically developed on opposite sides of the specimen. There are also weak, rounded, fold-like ribs crossing the venter and extending onto the outer flanks. C.93578 (Fig. 9) has a similar diameter. The style of ribbing typical of the septate whorls extends onto the adapical part of the body chamber. The inner ventrolateral tubercles are highly spinose here. On the adoral part of the body chamber the ribs become weaker and very widely spaced while the umbilical tubercles become weak, bullate, unevenly developed structures which may be twisted backwards. Flank ribbing is virtually absent here though prominent, bullate inner ventrolateral tubercles persist and pass over the ventrolateral shoulders as narrow, rib-like structures. The sutures in this material are rather florid. The lateral lobe is very wide and subdivided by a broad but fairly low median element.

REMARKS. The lectotype of *P. footeanum* (selected by Wright & Kennedy 1981: 82) is the specimen figured by Stoliczka (1864: pl. 52, figs 1a–c) (see also Kennedy *et al.* 1987: text-fig. 4). It has a diameter of over 250 mm. The whorl section is quadrate. The ribs are generally radial and of uneven development on the later whorls. They arise from umbilical bullae but some fade before reaching the prominent inner ventrolateral tubercles. Outer ventrolateral tubercles are persistent but adorally tend to merge with the bullate inner ventrolateral tubercles to form a ventrolateral rib-like structure. A similar ornament is seen on a number of fragmentary body chambers from Angola described by Howarth (1985: 98, figs 31–33). The ornament of the lectotype and the Angolan specimens agrees well with that in the later whorls of the Nigerian material. The collection from Angola also includes one specimen showing the ornament of the middle whorls (C.81073, Howarth 1985, fig. 30). This individual closely resembles C.93362 from Nigeria though the latter has outer ventrolateral tubercles located a little further from the siphonal line and often elongated obliquely forwards.

Ammonites pedroanus White (1887: 212, pl. 22, figs 1, 2) is a synonym of *P. footeanum* (see also Chancellor 1982: 94; Bengtson 1983: 16; Howarth 1985: 98). Chancellor (1982: 95) suggested that *P. paganum* Reyment was also conspecific, along with the Nigerian specimen figured by Woods (1911: 283, pl. 23, figs 1, 2). *P. paganum* is here considered to be a distinct species while Woods' material belongs in *P. flexuosum* (see below).

The *Pseudaspidoceras* cf. *footeanum* of Wright & Kennedy (1981: 82, pl. 21, fig. 3) has whorls distinctly higher than broad. Its umbilical and inner ventrolateral tubercles are larger than those of the lectotype and the outer ventrolateral tubercles are closer to the siphonal line. In its smooth venter and prominent inner ventrolateral tubercles it is like *P. flexuosum*. The specimen is reported as coming from a stratigraphical level relatively high in the Lower Turonian (*Mammites nodosoides* Zone at Dover) whereas the Nigerian material is from the Upper Cenomanian. The *Pseudaspidoceras* sp. aff. *footeanum* of Matsumoto (*in* Matsumoto *et al.* 1978: 17, pl. 5, fig. 1) from Japan is a fragment only

doubtfully referrable even to the genus.

Pseudaspidoceras footei var. *grecoi* Collignon (1965*b*: 176, pl. E, figs 1a, b; Collignon & Roman *in* Amard *et al.* 1981: pl. 5, figs 1a, b) is a highly evolute form with a subquadrate whorl section a little higher than broad. Narrow, radial ribs, effaced in the mid-flank, arise from umbilical bullae and bear prominent inner ventrolateral tubercles. Intercalated ribs arise upon the outer flanks. All the ribs cross the ventrolateral shoulders but do not reach the siphonal line. In its whorl section and ornament this form is rather closer to *P. paganum* (see below) than to *P. footeanum*.

Pseudaspidoceras reesidei Benavides-Cáceres (1956: 468, pl. 54, figs 1–4; text-fig. 51) is a moderately depressed species with an ornament similar to that in *P. footeanum*. The former is, however, less evolute and its lateral lobe is subdivided by a very low median element; in these respects it more resembles *Morrowites*.

The *Acanthoceras*(?) cf. *footeanus* of Choffat (1898: 66, pl. 6, fig. 5) seems to be adult at a diameter of less than 90 mm. There are strong, rectiradiate ribs on the phragmocone while the mainly smooth body chamber has weak, irregularly developed, closely spaced ribs. The suture is unknown. This form resembles the adults of *P. pseudonodosoides* from Nigeria described above.

Pseudaspidoceras paganum Reyment, 1954*a*

Figs 15, 16, 22, 23

1954*a* *Pseudaspidoceras paganum* Reyment: 253, pl. 4, fig. 1; text-figs 3h, 4.
1955 *Pseudaspidoceras curvicostatum* Reyment: 55, pl. 11, fig. 1; pl. 12; text-fig. 24.
1989 *Pseudaspidoceras paganum* Reyment; Meister: 6 (*pars*), pl. 1, fig. 1; text-fig. 3.
1990 *Pseudaspidoceras* cf. *flexuosum* Powell; Zaborski: fig. 23 (only).
1991 *Pseudaspidoceras flexuosum* Powell; Courville *et al.*: 1041.

MATERIAL AND OCCURRENCE. Ten specimens, C.91275, C.93331, C.93537, C.93918–9, C.93920, C.93924–6, from the Pindiga Formation, unit R (upper surface), Ashaka; C.93923, and the holotype (C.47422), are specimens collected loose from the Pindiga Formation, Pindiga but their matrix strongly suggests derivation from unit O there.

Table 3 Morphometric data for *Pseudaspidoceras paganum* Reyment, 1954a.

	D	Wb	Wh	U
C.93331	146	55 (38)	58 (40)	45 (31)
C.93924	143	48 (33.5)	50 (35)	53 (37)
C.93925	140	49 (35)	52 (37)	50 (36)
C.93537	135	46 (34)	50 (37)	52 (38·5)
C.93919	115	44 (38)	48 (39)	42 (36·5)

Dimensions (in mm). D, diameter; Wb, whorl breadth; Wh, whorl height; U, umbilical diameter. Figures in parentheses are dimensions as a percentage of the total diameter.

DESCRIPTION. The whorls are quadrate or, more usually, a little higher than broad. Maximum whorl breadth is at the level of the umbilical tubercles. The flanks converge slightly upon the flattened to broadly rounded venter. At diameters

of less than 7 mm the whorls are ovoid and smooth. By diameters of 20–25 mm there are narrow, fairly sharp, radial to slightly convex ribs. They mostly arise at feeble umbilical bullae and bear weak inner ventrolateral tubercles. They curve forwards over the ventrolateral shoulders and terminate in pronounced outer ventrolateral tubercles which are elongated obliquely forwards. By diameters of 40–45 mm the outer ventrolateral tubercles are more rounded in shape, there being 2 or 3 for each inner ventrolateral tubercle. At diameters of 50–60 mm the inner and outer ventrolateral tubercles are of equal strength. At larger diameters the ribs become unevenly developed. They are radial, convex or flexuous in shape but may be effaced in the mid-flank region. Most arise at variably developed umbilical bullae and all bear bulbous to spinose inner ventrolateral tubercles which become the most pronounced ornamental feature. Other ribs arise in the mid-flank region and there may be pairs of additional intercalated inner ventrolateral tubercles. Situated adoral of the inner ventrolateral are rounded to clavate outer ventrolateral tubercles. There are usually 1–3 pairs of additional outer ventrolateral tubercles between successive pairs of inner ventrolaterals. These tubercles are of variable strength and are sometimes asymmetrically developed. The inner and outer ventrolateral tubercles persist as discrete structures to the largest diameters seen, of nearly 150 mm. In the later growth stages there may be weak, fold-like structures upon the flanks between the main ribs.

REMARKS. Chancellor (1982: 95) suggested that *P. paganum* was a synonym of *P. footeanum*. The two are similar but whorl breadth generally exceeds whorl height in the latter while the opposite condition prevails in *P. paganum*. The inner and outer ventrolateral tubercles also persist as discrete structures to larger diameters in *P. paganum*; in *P. footeanum* these tubercles take the form of bullate swellings on ventrolateral rib-like structures in the later growth stages. *P. paganum* has a more rounded venter and its sutural elements are more elongate and finely subdivided.

Pseudaspidoceras curvicostatum Reyment (1955: 55, pl. 11, fig. 1; pl. 12; text-fig. 24) is a synonym of *P. paganum* (see also Chancellor 1982: 92). The holotype (C.54801) is from the Abazi River at Ezillo in south-eastern Nigeria. The species was distinguished mainly on the basis of its strongly curved ribs. As described above, however, this condition is also found in the later growth stages in *P. paganum*.

The *Acanthoceras* cf. *footeanum* (Stoliczka) of Eck (1914: 196, pl. 17, figs 1, 2) is represented by a poorly preserved specimen with whorls higher than broad and marked inner and outer ventrolateral tubercles up to a diameter of at least 50 mm. This form may be most closely related to *P. paganum*. As mentioned above *P. footei* var. *grecoi* Collignon also shows similarities with *P. paganum*.

Specimens referred to *P. paganum* by Barber (1957: 9) are better placed in *P. flexuosum* (see below). Meister (1989: 8) reported *P. paganum* from units O and R at Ashaka. All members of the genus found in unit O during the present work, however, are best referred to *P. footeanum*. The *P. flexuosum* of Courville *et al.* (1991) are *P. paganum*.

Pseudaspidoceras flexuosum Powell, 1963

Figs 11–13, 17, 18, 20, 21

1902 *Mammites footeanus* Stol. spec. Petraschek: 144, pl. 9, fig. 1.
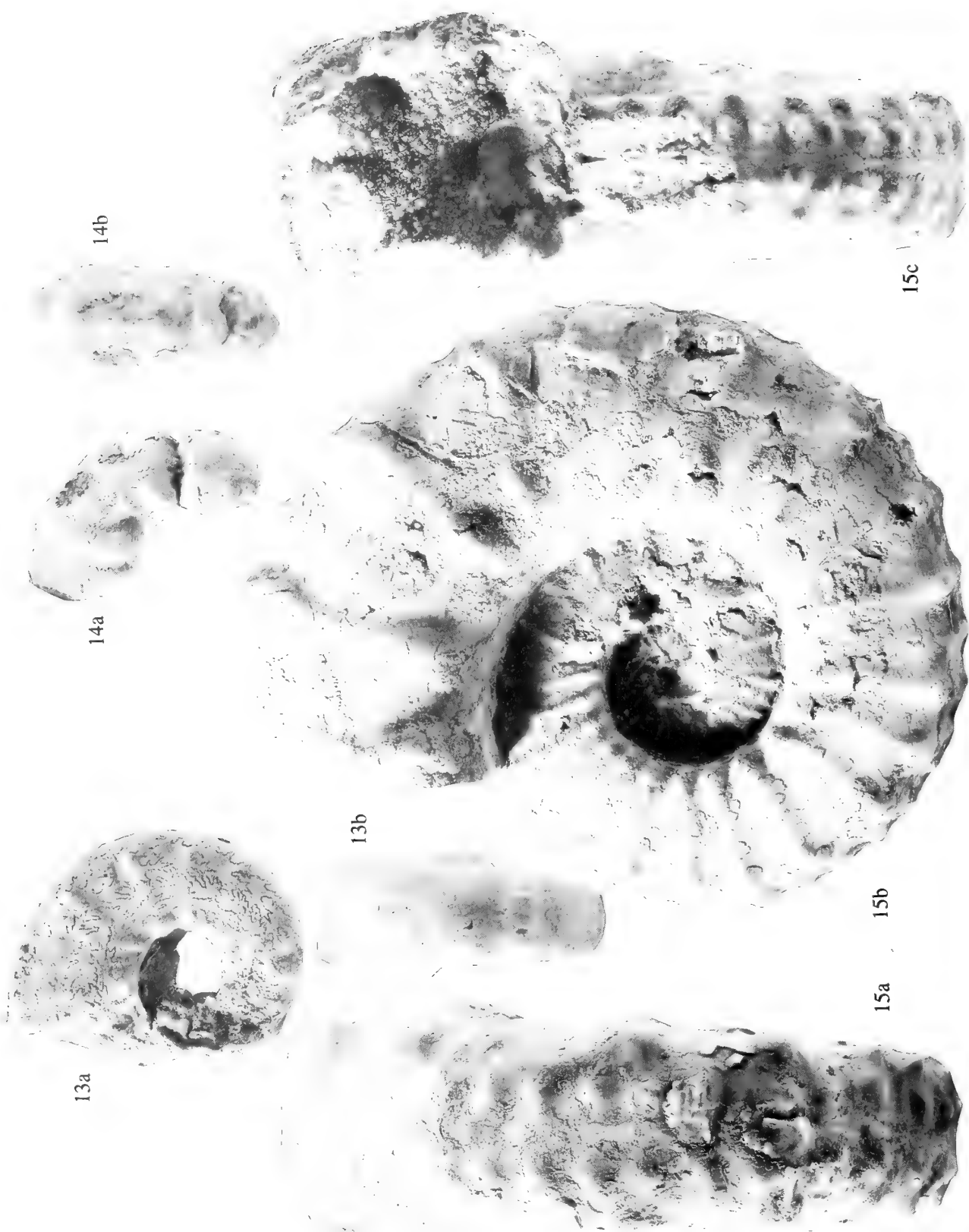
Fig. 13a, b *Pseudaspidoceras flexuosum* Powell. Pindiga Formation, unit T2, Ashaka. C.93563, x1.
Fig. 14a, b *Pseudaspidoceras pseudonodosoides* (Choffat). Pindiga Formation, unit M, Pindiga. C.93594, x1.
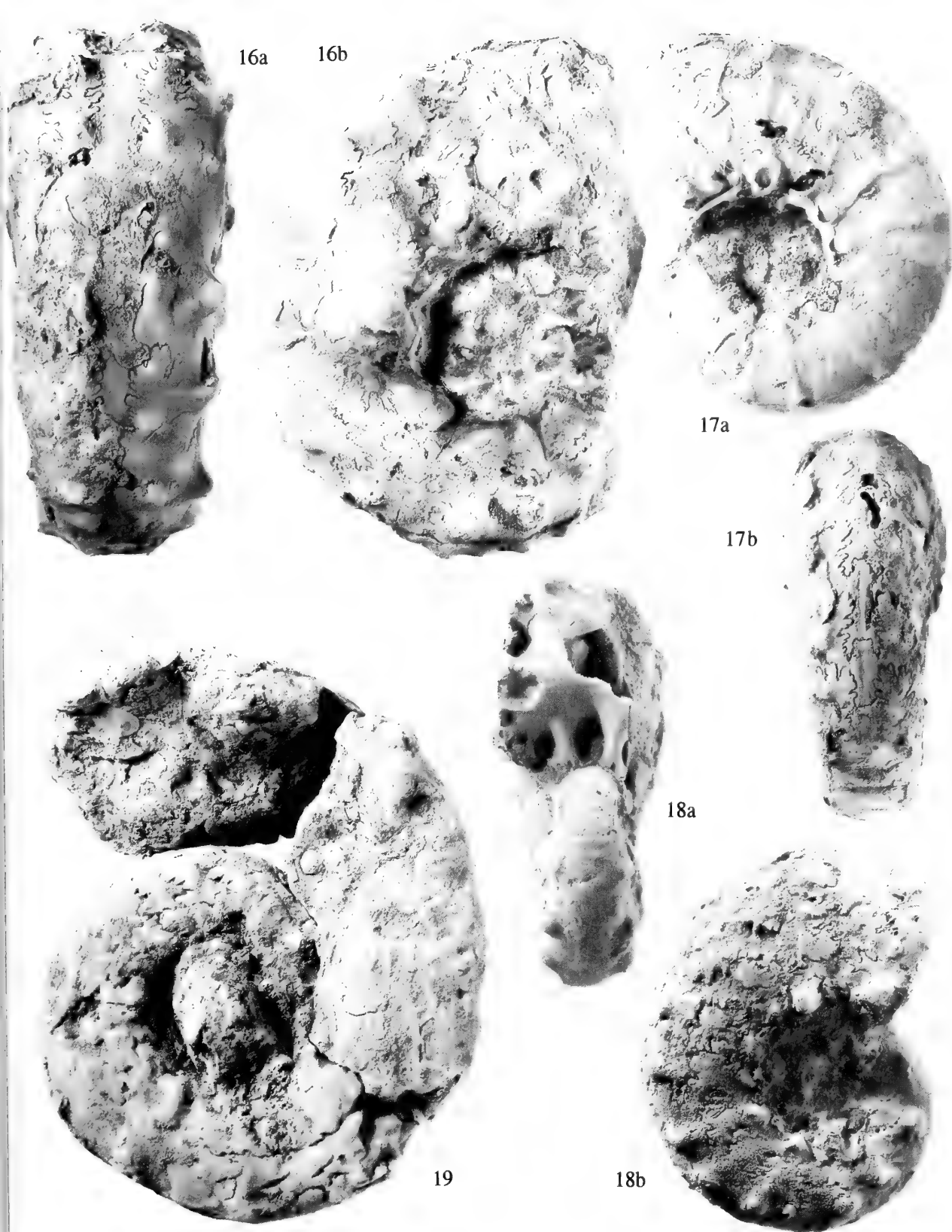
g. 16a, b *Pseudaspidoceras paganum* Reyment. Pindiga Formation, unit R, Ashaka. C.93331, x0.67. **Figs 17, 18** *Pseudaspidoceras flexuosum* Powell. Fig. 17, a, b, Pindiga Formation, unit T2, Ashaka. C.93366, x1. Fig. 18a, b, collected loose from the Pindiga Formation, Pindiga. C.91276, x1. **Fig. 19** *Burroceras*? sp. Pindiga Formation, unit H, Pindiga. C.93369, x1.
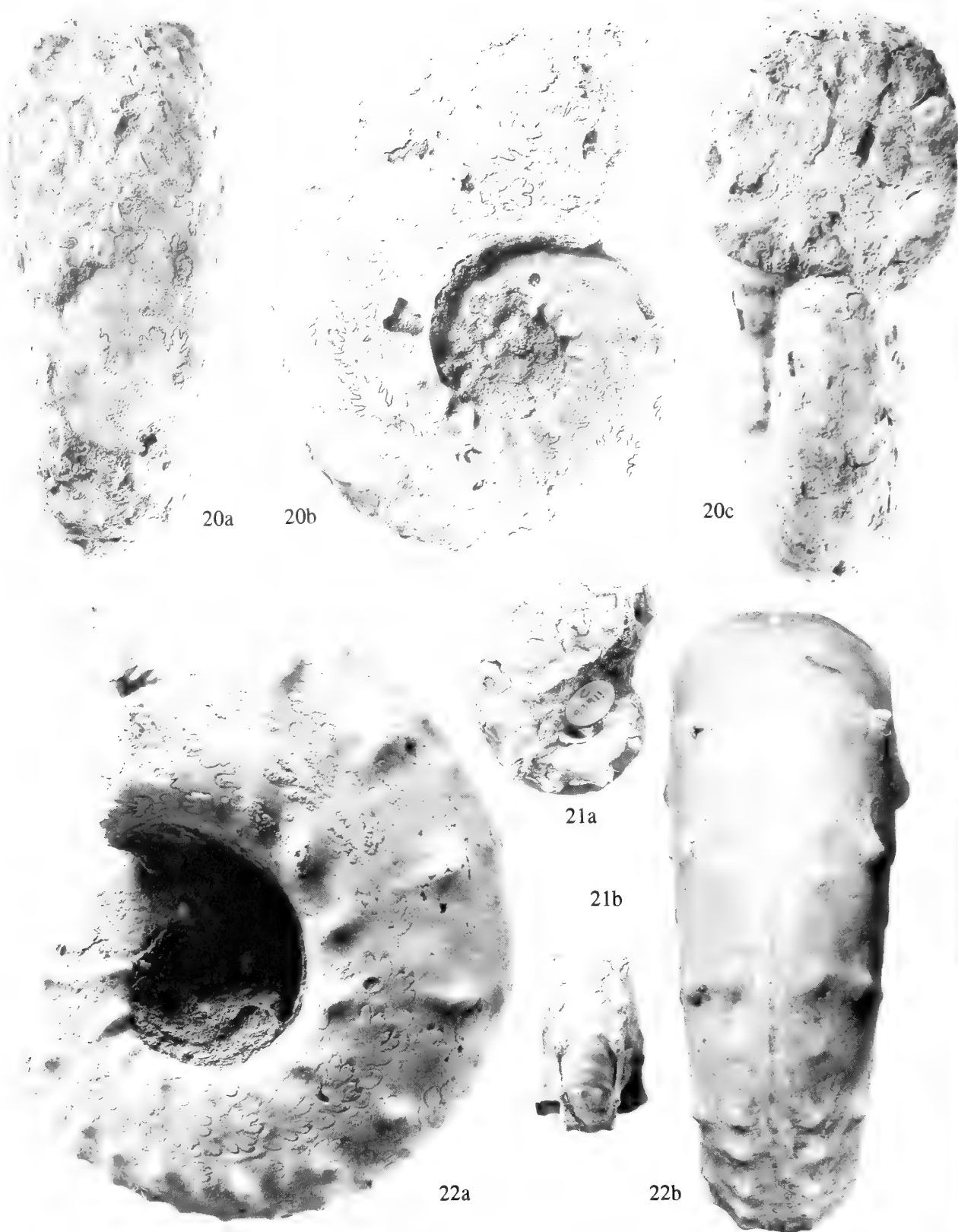
Figs 20, 21 *Pseudaspidoceras flexuosum* Powell. Pindiga Formation, unit T2, Ashaka. Fig. 20a–c, C.93367, x1. Fig. 21a, b, C.93911, x1.
Fig. 22a, b *Pseudaspidoceras paganum* Reyment. Pindiga Formation, unit R, Ashaka. C.93919, x1.

1911 *Mammites (Pseudaspidoceras)* sp. Woods: 283, pl. 23, figs 1, 2.

1920 *Pseudaspidoceras* aff. *pedroanum* (White); Böse: 209, pl. 13, fig. 1; pl. 15, fig. 1.

1957 *Pseudaspidoceras paganum* Reyment; Barber: 9, pl. 1, figs 1, 2; pl. 25, figs 5–7.

1963 *Pseudaspidoceras flexuosum* Powell: 318, pl. 32, figs 1, 9, 10; text-figs 2a–c, f, g.

1965a *Kamerunoceras (Ampakabites) auriculatum* Collignon: 29, 31, pl. 388, fig. 1662; pl. 389, fig. 1664.

1972 *Ampakabites collignoni* Cobban & Scott: 81, pl. 29, figs 1–3; text-figs 39, 40.

1987 *Pseudaspidoceras flexuosum* Powell; Kennedy, Wright & Hancock: 34, pl. 2, figs 1–4, 8–13, 16, 17; text-figs 3A–C, 5, 6C, D, 7A–C.

1989 *Pseudaspidoceras barberi* Meister: 8, pl. 1, fig. 2; pl. 2, figs 2, 5; text-fig. 4.

1989 *Pseudaspidoceras flexuosum* Powell; Cobban, Hook & Kennedy: 41, fig. 91L.

1990 *Pseudaspidoceras* cf. *flexuosum* Powell; Zaborski: fig. 24 (only).

1990 *Pseudaspidoceras flexuosum* Powell; Amêdro *in* Robaszynski *et al.*: 264, pl. 17, fig. 1; pl. 18, fig. 1.

1992 *Pseudaspidoceras barberi* Meister; Courville: pl. 2, fig. 2.

MATERIAL AND OCCURRENCE. Nineteen specimens, C.93366–8, C.93560–7, C.93911–7, from the Pindiga Formation, unit T2, Ashaka; C.91276, collected loose from the Pindiga Formation, Pindiga.

Table 4 Morphometric data for *Pseudaspidoceras flexuosum* Powell, 1963 (see also Barber 1957: 9).

	D	Wb	Wh	U
C.93367	112	42 (37·5)	46 (41)	35 (31)
C.93567	98	42 (43)	42 (43)	30 (31)
C.93368	91	38 (42)	43 (47)	26 (28·5)
C.93366	83	31 (37)	40 (48)	25 (30)
C.93566	81	28 (34·5)	38 (47)	25 (31)
C.91276	75	29 (39)	34 (45)	–
C.93565	72	32 (44)	34 (47)	–
C.93564	66	28 (42)	30 (45)	20 (30)
C.93562	50	20 (40)	22 (44)	–

Dimensions (in mm). D, diameter; Wb, whorl breadth; Wh, whorl height; U, umbilical diameter. Figures in parentheses are dimensions as a percentage of the total diameter.

DESCRIPTION. Although whorl height is generally a little to markedly greater than whorl breadth, exceptional specimens show quadrate whorls. The latter tend to have rather flattened venters but in most cases the flanks are flattened and the venters broadly rounded in this material.

C.93560 (Fig. 11) shows the ornament at a diameter of less than 30 mm. There are 10–11 ribs in the last whorl which arise at umbilical bullae. They bear prominent, bulbous to clavate inner ventrolateral tubercles at which they loop forwards over the venter and branch into pairs. The adapical rib of each pair bears weak, nodate outer ventrolateral tubercles located close to the siphonal line; the adoral rib is a simple untuberculated structure curved convexly forwards.

The ornament of the middle whorls is variable. The ribs may be fairly broad and radial in disposition, distinctly curved, or flexuous. They may be effaced in the mid-flank region and often branch. All the main ribs arise at umbilical tubercles, which are often of variable strength. They may be bullate or spinose and twisted backwards. Each rib bears a prominent, bulbous to bullate inner ventrolateral tubercle, these structures outnumbering the umbilical tubercles where the ribs branch. In other cases, ribs fade before reaching the ventrolateral shoulder and here the umbilical tubercles outnumber the inner ventrolaterals. Across the venter each rib bears a pair of weak outer ventrolateral tubercles located close to the siphonal line and a little adoral of the inner ventrolaterals. There may be additional weak intercalated ventral ribs curved convexly forwards and without tubercles, or additional pairs of isolated outer ventrolateral tubercles may occur.

The outer ventrolateral tubercles may already have disappeared at diameters of about 50 mm or they may persist until diameters in excess of 100 mm. After they have faded the venter is broadly arched and flanked by prominent inner ventrolateral tubercles. Weak, convexly curved ventral ribs may persist up to diameters as large as 120 mm. No adult body chamber is available. The sutures are complex with narrow, elongate, finely subdivided saddles. The lateral lobe is broad and divided, often asymmetrically, by a narrow, elongate median element.

REMARKS. Chancellor (1982: 95) suggested that the Nigerian ammonite described by Woods (1911: 283, pl. 23, figs 1, 2) (specimen B3240 in the Sedgwick Museum, Cambridge) was referrable to *P. paganum* and that this species was a probable synonym of *P. footeanum*. He doubted, however, that all the material referred to *P. paganum* by Barber (1957: 9) belonged in *P. footeanum*. Similarly, Kennedy *et al.* (1987: 68) thought that Barber's material was in part *P. flexuosum*. Here, all this Nigerian material is included in *P. flexuosum*, along with *P. barberi* Meister (1989: 8).

The most detailed previous description of *P. flexuosum* was based on a large collection from west Texas (Kennedy *et al.* 1987: 34). The early whorls in the Nigerian material are entirely comparable with those in the Texan specimens. The minor differences in the later growth stages of the Nigerian forms, occasional large whorl breadth and relatively coarse flank ribbing, can be ascribed to individual variation. Considerable inconsistency is displayed in these features by the Ashaka specimens though they all come from a single 5–6 cm calcareous clay horizon. The variation is sufficient to encompass Woods' and Barber's material. *P. paganum* has consistently broader whorls, more pronounced, spinose and persistent outer ventrolateral tubercles located a little further away from the siphonal line, and a less complex suture. Courville (1992: 423–424) reported *Pseudaspidoceras barberi* (= *P. flexuosum*) from unit U (his level 32) at Ashaka. The fauna described by him, however, is that of unit T2 (upper part of his level 30).

Genus *BURROCERAS* Cobban, Hook & Kennedy, 1989

TYPE SPECIES. *Burroceras clydense* Cobban, Hook & Kennedy, 1989; by original designation.

REMARKS. *Burroceras* was proposed by Cobban, Hook & Kennedy (1989: 37) for material from New Mexico transitional in form and age from *Euomphaloceras* to *Pseudaspidoceras*. It combines the shell form and suture pattern of *P.*
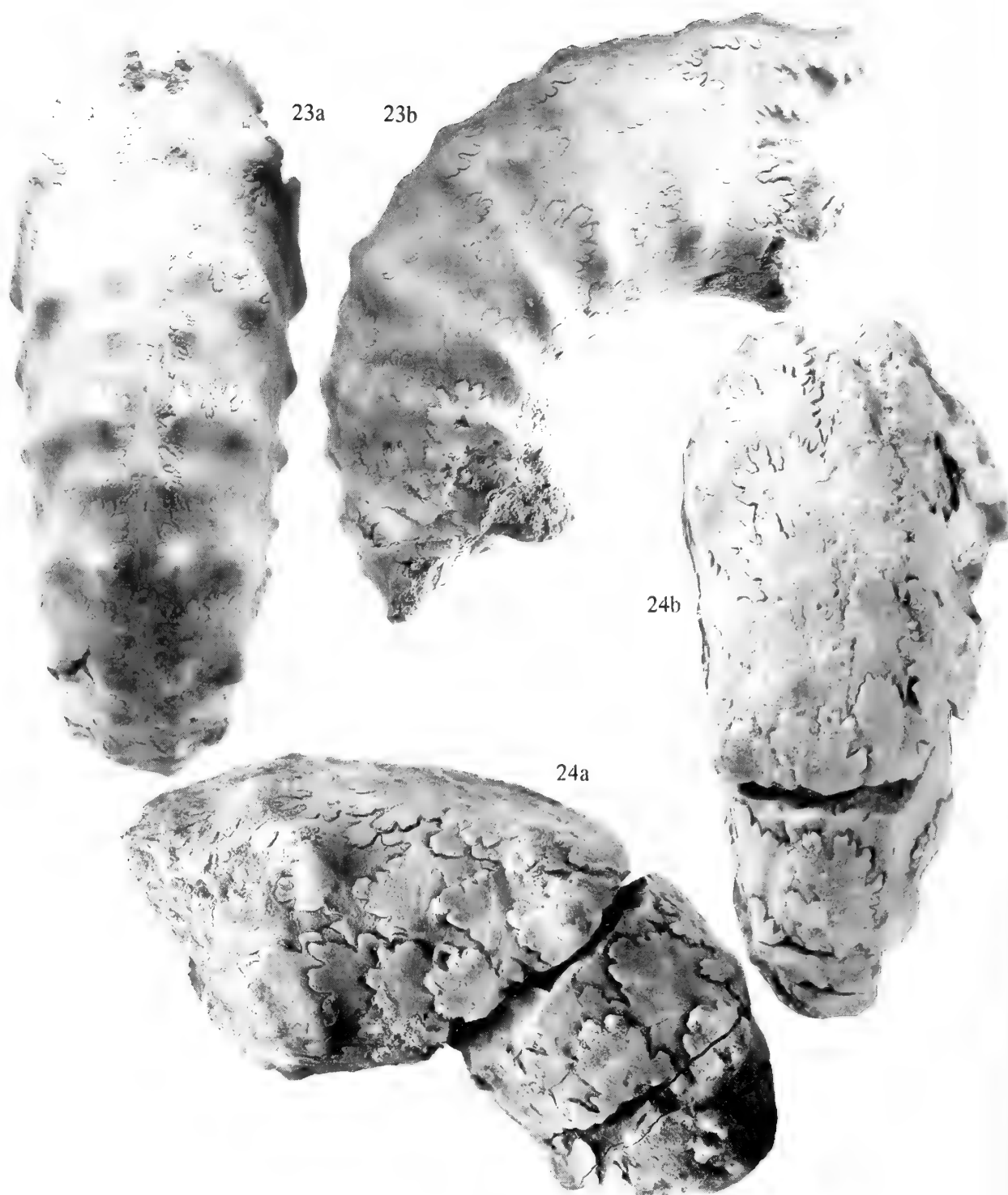
Fig. 23a, b *Pseudaspidoceras paganum* Reyment. Pindiga Formation, unit R, Ashaka. C.93918, x1.
Fig. 24a, b *Burroceras*? sp. Pindiga Formation, unit F, Ashaka. C.93572, x1.

pseudonodosoides with the tubercle distribution of *E. euomphalum* (Sharpe), siphonal tubercles being present. Three species were identified, all of Late Cenomanian age: *B. clydense* Cobban, Hook & Kennedy (1989: 38, figs 38, 79D–G, N–T) with a prominent ornament including ventro-lateral horns and marked siphonal clavae; *B. irregulare* Cobban, Hook & Kennedy (1989: 38, figs 39, 80S–V) with an ornament of highly irregular strength; and *B. transitorium* Cobban, Hook & Kennedy (1989: 39, figs 40, 79A–C, 80D–R) distinguished chiefly by its weak siphonal ornament.

Burroceras? sp.   Figs 19, 24

MATERIAL AND OCCURRENCE. Three specimens, C.93369–70, from the Pindiga Formation, unit H, Pindiga; C.93572, from the Pindiga Formation, unit F (upper part), Ashaka.

DESCRIPTION. C.93370 is part of a body chamber with a diameter of some 120 mm. Umbilical bullae give rise to robust flank ribbing. There are strong, rather clavate inner ventrolateral tubercles but the ventral area is poorly pre-served making identification of any ornament difficult. C.93369 (Fig. 19) is a more complete specimen with a diameter of 125 mm and consisting of one septate whorl and about half a whorl of body chamber. There are narrow, radial ribs of moderate strength on the septate whorl which arise from umbilical bullae and bear prominent inner ventrolateral tubercles. Again the ventral area is poorly preserved.

C.93572 (Fig. 24) is part of a septate whorl with a diameter of about 130 mm. Whorl breadth slightly exceeds whorl height. The flanks are flattened and the venter broadly rounded. There are distant umbilical bullae of moderate strength giving rise to low, rounded ribs which weaken in the mid and outer flank regions. They bear fairly strong, rounded inner ventrolateral tubercles at which they bend forwards and become weak, broad structures before terminating at smaller, rounded outer ventrolateral tubercles. There are vague traces of siphonal swellings but it is difficult to determine if they are real or preservational features. The suture shows a broad, low median element subdividing the lateral lobe.

REMARKS. This material, from horizons low in the Ashaka and Pindiga sections, differs from the earliest *Pseudaspi-doceras*, *P. pseudonodosoides*, in the retention of discrete outer ventrolateral tubercles until larger diameters. Unfortu-nately, positive identification of siphonal ornament is not possible in these specimens and consequently they can only be tentatively referred to *Burroceras*. Of the three species proposed by Cobban *et al.* (1989) in New Mexico the present material most closely resembles *B. transitorium* in ornamen-tal style and suture pattern. In particular the siphonal tubercles, located on a siphonal ridge which disappears on the adult body chamber, are very weak, often barely noticeable in this species.

STRATIGRAPHICAL DISCUSSION

Several biostratigraphical schemes based on ammonites have been put forward for the Cenomanian-Turonian beds in north-eastern Nigeria (see Reyment 1954a, 1954b, Barber 1957, Wozny & Kogbe 1983, Popoff *et al.* 1986, Meister 1989, Zaborski 1990, including a review, Courville *et al.* 1991).

That proposed by Zaborski (1990) is maintained here. Briefly, five biozones were recognized, all defined at their bases by the appearances of the nominal species. They are, from oldest to youngest: a Zone of *Nigericeras gadeni*; a Zone of *Vascoceras cauvini*; a Zone of *Vascoceras proprium*, defined at its base by the appearance of *V. proprium cos-tatum*, two further subspecies, *V. proprium globosum* (basal Proprium to basal Nigeriensis Zone) and *V. proprium pro-prium* (lower Nigeriensis Zone), being recognizable in the region; a Zone of *Pseudotissotia nigeriensis*; and a Zone of *Wrightoceras wallsi* Reyment. The stratigraphical distribution of *Burroceras*(?) and the various species of *Pseudaspidoceras* within this framework is as follows: *Burroceras*(?), lower part of the Cauvini Zone; *P. pseudonodosoides*, upper part of the Cauvini Zone; *P. footeanum*, lower part of the Proprium Zone; *P. paganum*, basal Nigeriensis Zone; and *P. flexu-osum*, lower part of the Nigeriensis Zone (see Fig. 1).

The best dated occurrences of *Pseudaspidoceras* elsewhere in the world are in New Mexico and west Texas (see Hook & Cobban 1981, Cobban & Hook 1983a, 1983b, Cobban 1984, Kennedy *et al.* 1987, Cobban *et al.* 1989). In these areas only *P. pseudonodosoides* and *P. flexuosum* are known, but in south-western New Mexico *Burroceras* is also present. The following biozones have been recognized in the Upper Cen-omanian and Lower Turonian there (Cobban *et al.* 1989):

Lower Turonian	Zone of *Mammites nodosoides* (Schlüter)
	Zone of *Vascoceras birchbyi* (Cobban & Scott)
	Zone of *Pseudaspidoceras flexuosum* Powell
Upper Cenomanian	Zone of *Neocardioceras juddii* (Barrois & Guerne)
	Zone of *Burroceras clydense* Cobban, Hook & Kennedy
	Zone of *Sciponoceras gracile* (Schumard)
	Zone of *Metoicoceras mosbyense* Cobban
	Zone of *Calycoceras canitaurinum* (Haas)

Burroceras clydense is the earliest known member of its genus. *B. irregulare* and *B. transitorium*, along with *Pseu-daspidoceras pseudonodosoides*, are Juddii Zone forms. *P. flexuosum* characterizes the lowest Turonian zone recogniz-able. There is, however, an hiatus horizon at the top of the Juddii Zone in south-western New Mexico and it is at this level that *P. pseudonodosoides* occurs; latest Cenomanian beds equivalent in age to the Zone of *Nigericeras scotti* Cobban in south-east Colorado and north-east New Mexico are missing.

The Gracile Zone in New Mexico can be correlated with the Nigerian Gadeni Zone as both contain *Metoicoceras geslinianum* (d'Orbigny) (see Cobban *et al.* 1989, Zaborski 1990). The Nigerian Cauvini Zone is, at least in part, the equivalent of the Juddii Zone as developed in south-west New Mexico. The *Burroceras*(?) in unit F at Ashaka and unit H at Pindiga cannot be identified to species level but appears closest to *B. transitorium*, a Juddii Zone form. Equivalents of the Clydense Zone cannot therefore be positively identified in north-east Nigeria at present. *Burroceras*(?) in Nigeria is associated with early *Vascoceras cauvini* which may closely

resemble *V. barcoicense* Choffat *exile* Cobban, Hook & Kennedy (1989: 47, figs 47, 87Q–S, 89M–GG), at least in the middle whorls, but the latter ranges from the Clydense to the Juddii Zone in New Mexico.

Units K and M at Ashaka and M and N at Pindiga, which contain the known stratigraphical range of *P. pseudono-dosoides*, can be correlated with the upper part of the Juddii Zone in south-western New Mexico. Lying disconformably above in the latter region are sandy beds containing the *P. flexuosum* fauna. This species occurs in unit T2 at Ashaka. As explained below, there are no equivalents in south-western New Mexico of units N to T1 at Ashaka. At Pindiga the corresponding part of the sequence is largely unexposed, though units O and P comprise a portion of it. The missing part of the sequence in south-western New Mexico corresponds to that containing *P. footeanum* and *P. paganum* in Nigeria. In unit T2 at Ashaka *P. flexuosum* is accompanied by large numbers of *Pseudotissotia nigeriensis* and in addition *Vascoceras proprium proprium*, *V. obscurum*, *Thomasites gongilensis*, *Choffaticeras* sp., *Watinoceras* aff. *coloradoense* and *Wrightoceras munieri* (= *W. wallsi* of Meister 1989: pl. 28, fig. 2). This fauna is of closely similar age to that from west Texas described by Kennedy *et al.* (1987) and taken to characterize the basal Turonian Zone of *Pseudaspidoceras flexuosum* there. Apart from *P. flexuosum*, *Thomasites*, *V. proprium proprium* and *W. munieri* are notable common elements. The appearance of *P. flexuosum* in the west Texas-New Mexico area was suggested as a marker for the base of the Turonian stage by Kennedy (1984) (see also Cobban 1984, Birkelund *et al.* 1984: 12). Hancock (1984, 1991) further suggested that *V. proprium proprium* might perform the same stratigraphical function but at Ashaka this form occurs in unit T1, immediately below the first occurrence of *P. flexuosum*. On the basis of the appearance of *P. flexuosum*, the base of the Turonian coincides with the base of unit T2 at Ashaka. The top of unit T1 is a discontinuity surface, overlain by a thin layer of diagenetic gypsum, while unit T2 which has a high content of glauconite and phosphatic matter is condensed. Construction of a correlation line between the Ashaka and Pindiga sections indicates that the Cenomanian-Turonian boundary in the latter occurs about 56 m above the base of the lowest limestone unit (A, see Fig. 1). This portion of the section is unexposed. A single specimen of *P. flexuosum* (C.91276, Fig. 18) has been found at Pindiga but its precise horizon is unknown.

Courville *et al.* (1991), it should be noted, placed the Cenomanian-Turonian boundary within what is regarded here as the Upper Cenomanian since specimens of *P. paganum* from both northern and southern Nigeria were misidentified as *P. flexuosum*. Their *P. barberi* are synonymous with *P. flexuosum*.

The Cenomanian-Turonian boundary in north-eastern Nigeria occurs in the lower part of the Nigeriensis Zone. The earliest forms here referred to *Pseudotissotia nigeriensis* (from unit R at Ashaka and unit O at Pindiga), however, do not develop the typically tricarinate venter until relatively large diameters of 50–60 mm. These individuals are morphologically intergradational with their prolific associate *Thomasites gongilensis*. There is little doubt that *P. nigeriensis* was derived from the latter species (see also Barber 1957, Meister 1989). A clear distinction between the two cannot be made at these stratigraphical levels. Meister (1989) evidently referred the entire assemblage from unit R at Ashaka to *T. gongilensis*. Undoubted examples of *P. nigeriensis* do, nevertheless,

appear before *Pseudaspidoceras flexuosum*; they are abundant in unit T1 at Ashaka. It may also be noted here that the identification of the Zone of *Wrightoceras wallsi* at Ashaka and Pindiga by Zaborski (1990) was based on previous reports of the occurrence of that species (see Barber 1957, Popoff *et al.* 1986). Its presence has not been confirmed in this work and the zone is not, therefore, indicated in Fig. 1. Identifications of *W. wallsi* from unit T at Ashaka by Meister (1989) are here regarded as dubious; the material is, at least in part, *W. munieri*.

If unit T2 at Ashaka represents the basal Turonian then *Pseudaspidoceras footeanum* and *P. paganum* are Late Cenomanian in age. *P. footeanum* was assigned to the Lower Turonian in Angola by Howarth (1985). Bengtson (1983: 44) also recorded the species from the Lower Turonian in Brazil but, in addition, listed similar forms from the high Cenomanian. Records of *P. footeanum*, however, reveal little accurate dating against other ammonites. The Nigerian examples, from unit O at Ashaka, come from a stratigraphical level higher than that of the Juddii Zone but lower than that of the Flexuosum Zone in south-western New Mexico. Unit O contains an ammonite assemblage dominated by species of *Vascoceras*. Prominent within the fauna are multituberculated forms with simplified sutures (*Nigericeras* and *Paramammites* of Barber 1957, and *Vascoceras costatum* (Reyment) and *Paramammites subconciliatus* (Choffat) of Meister 1989). This group shows a morphological gradation into smoother ammonites referrable to *Vascoceras nigeriense* Woods (1911: 281, pl. 21, fig. 6; pl. 22, figs 2, 3). The more strongly ornamented examples frequently resemble *Nigericeras scotti* Cobban (1971: 18, pl. 9, figs 1–4; pl. 18, figs 1–9; text-figs 15–19), the nominal species for the topmost Cenomanian zone recognizable in south-west Colorado and north-east New Mexico.

The *Pseudaspidoceras* cf. *footeanum* of Wright & Kennedy (1981: 82, pl. 21, fig. 3) is reported as coming from a much higher stratigraphical level (the *Mammites nodosoides* Zone of southern England) but, as mentioned above, probably does not belong in *P. footeanum*.

The exact stratigraphical level of the holotype of *P. paganum* at Pindiga is uncertain. It is preserved in a hard, orange-weathering limestone matrix closely matching unit O there. The same is true of specimen C.93923, collected loose at Pindiga. This bed is their probable source, especially as it contains an ammonite fauna otherwise identical to that of unit R at Ashaka, in which *P. paganum* is known to occur: *Thomasites gongilensis* at its acme, *Vascoceras proprium globosum* and the earliest *Pseudotissotia nigeriensis*. Units O and P are the 'Gombeoceras Limestones 1 and 2' of Barber (1957) which make up his Zone of *Paravascoceras costatum* (Reyment). Barber (1957: table 3) listed a number of species additional to those mentioned above which were said to characterize these horizons. These forms, however, are probably derived from loose limestone blocks found scattered in gullies and fields at a stratigraphical level between units N and O at Pindiga. These blocks yield elements of the fauna characterizing the Proprium Zone elsewhere including *Vascoceras nigeriense*.

Pseudaspidoceras pseudonodosoides is well dated in Israel where it is found in the *Vascoceras cauvini* Zone (Freund & Raab 1969), a correlative of the Juddii Zone in north-west Europe, and in the New World (Lewy *et al.* 1984). This stratigraphical occurrence is in accord with that in north-eastern Nigeria. In Portugal the species occurs at the base of

the equivalent of the Juddii Zone but is recorded as ranging into the Lower Turonian (Berthou 1984, Berthou *et al.* 1985). *P. footeanum* is indicated as occurring low in the Juddii Zone. Similarly, in Israel Freund & Raab (1969) indicated both *P. footeanum* and *P.* cf. *P. paganum* as coming from the Cauvini Zone alongside *P. pseudonodosoides*. These species have a clear stratigraphical separation in north-eastern Nigeria and such records require confirmation.

Amêdro (*in* Robaszynski *et al.* 1990: 264) listed the order of stratigraphical occurrence of species of *Pseudaspidoceras* as: *P. pseudonodosoides* (Juddii Zone), *P. flexuosum* (basal Turonian) and *P. footeanum* (Nodosoides Zone). This interpretation seems to have been influenced by the description of *P.* cf. *footeanum* from the Nodosoides Zone by Wright & Kennedy (1981). However, as mentioned above, this specimen is closer to *P. flexuosum* but, even so, appears to occur anomalously high.

The expanded sequences across the Cenomanian-Turonian boundary in north-eastern Nigeria provide the best documented details available to date concerning the stratigraphical distribution of *Pseudaspidoceras* as a whole. Clearly the genus has great potential value in detailed correlation at these levels. Its occurrence in north-eastern Nigeria can be summarized as follows: *P. pseudonodosoides* occurs high in the Cauvini Zone equivalent to the upper part of the Juddii Zone elsewhere in the world and is thus of Late Cenomanian age; *P. footeanum* occurs in the lower part of the Proprium Zone, probably at a level equivalent to the highest Cenomanian Scotti Zone in parts of Colorado and New Mexico; *P. paganum* occurs in the basal part of the Nigeriensis Zone just below the Cenomanian-Turonian boundary; *P. flexuosum* occurs in the lower part of the Nigeriensis Zone equivalent to a level marking the basal Turonian in west Texas and New Mexico. Successive species show an increasing whorl compression, increasingly delicate ornament and an increasing sutural complexity.

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The pterodactyloids from the Purbeck Limestone Formation of Dorset

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CONTENTS

SYNOPSIS. The pterodactyloid fauna of the Tithonian-Berriasian Purbeck Limestone Formation of Dorset is revised taxonomically, using both previously described and new specimens. Three distinct taxa are present, namely two ctenochasmatids, *Gnathosaurus macrurus* comb. nov. based on a mandible and *Plataleorhynchus streptophorodon* gen. et sp. nov, based on a rostrum, together with an ornithocheirid '*Ornithocheirus*' sp. A, based on a second mandible. Other pterodactyloid material from Purbeck includes probable ctenochasmatid cervical vertebrae, and indeterminate pterodactyloid teeth, a radius, a metacarpal, a tibia and several wing phalanges, the latter including the type of *Doratorhynchus validus* which is a *nomen vanum*. The presence of an ornithocheirid in the Purbeck Limestone extends the history of this type of pterodactyloid back to the Jurassic-Cretaceous boundary and reinforces the view that the major diversification of this group took place in the Middle or Upper Jurassic.

INTRODUCTION

Since the middle of the nineteenth century, the Purbeck Limestone Formation has produced a rich continental vertebrate assemblage. Determinate pterosaur material has rarely been collected however, and only three isolated elements have been described or figured in the literature. Unfortunately, the taxonomic treatment of this material has not been entirely rational and it is necessary to review the systematic history of the Purbeck pterodactyloids to explain the systematic conclusions followed here. In 1868, H.G. Seeley obtained a pterodactyloid mandible and an elongate vertebra from a quarryman at a quarry near Langton Matravers, Purbeck, Dorset. Seeley (1869) listed these two specimens briefly, assigning them the name *Pterodactylus macrurus*. At

this stage, Seeley believed the vertebra to be a caudal of a long-tailed pterosaur, although he assigned it to *Pterodactylus*, a short-tailed genus. Owen (1870) figured a phalanx from 'near Swanage' as the new species *Pterodactylus validus*, but made no reference to it in the accompanying text. Seeley (1875) described the mandible and vertebra under Owen's species name *validus* despite the circumstances that firstly, his own *macrurus* was the senior specific name; secondly, Owen's figure had not been accompanied by a description; and thirdly, there was no basis for associating such disparate fragments. In his description of the vertebra, Seeley vacillated between identifying it as a caudal and as a cervical. Seeley also concluded that a new generic category was required for morphological and geographical reasons, and created the genus *Doratorhynchus* for these specimens. This aggregation of the Purbeck material under the binomen

Doratorhynchus validus has been followed by most subsequent authors e.g. Woodward & Sherborn 1890, Seeley 1901, Plieninger 1929, Wellnhofer 1978 and Howse 1986. However, Delair (1958) had reseparated Owen's and Seeley's specimens, following Lydekker (1888) in referring only the phalanx to *Ornithocheirus validus*. Curiously however, Delair retained the binomen *Doratorhynchus validus* for Seeley's two specimens, thus creating the insupportable situation of two *validus* species existing in place of one.

By 1901, Seeley had confidently reidentified the elongate vertebra as a cervical of a long-necked pterodactyloid, and noted the resemblance of this material to Solnhofen forms such as *Cycnorhamphus*, but no explicit comparisons were made. *Doratorhynchus validus* has subsequently remained in the literature as an enigmatic pterodactyloid, either placed doubtfully with the ornithocheirids, probably on the basis of the mandible (Wellnhofer 1978) or considered to be a possible early relative of the azhdarchids on the basis of the cervical vertebra (Howse 1986, Wellnhofer 1991a).

Recently, Angela C. Milner and one of the authors (ARM) recognised two undescribed pterodactyloid cranial fragments in blocks of Purbeck Limestone, in the collections of The Natural History Museum, London. The early history of the two specimens is unknown but they are recorded as having originally been part of the collection of the Corfe Castle Museum, the museum of the Purbeck Society. This collection passed to Dorset County Museum in 1894 when the Corfe Castle Museum closed (P.C. Ensom pers. comm.). It remained as a separate collection within the Dorset County Museum collections until part of it was purchased by the British Museum (Natural History) in 1958. The pterosaur specimens were subsequently shelved among the miscellaneous crocodilians, until recognised recently. Preparation and study of these two specimens has permitted a reassessment and systematic revision of the previously described Purbeck pterodactyloid material. The opportunity is also taken to record some of the other fragments of medium-large pterodactyloids collected at Purbeck over the last century. The material referred to in this work belongs to the following institutions (acronyms in parenthesis): Department of Palaeontology, The Natural History Museum (formerly British Museum (Natural History)), London (BMNH); Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich (BSPM); Dorset County Museum, Dorchester (DORCM); Sedgwick Museum, University of Cambridge (SMC).

STRATIGRAPHY

All the specimens reviewed in this work are from the Purbeck Limestone Formation of Dorset. Most were collected in quarries in the Swanage/Langton Matravers area, the exceptions being a fragmentary cervical vertebra, a metacarpal and some phalangeal material from Durlston Bay. None of the specimens is accompanied by precise data on the locality or horizon of collection. All of the Durlston Bay specimens and some from inland quarries are labelled as having been collected from the 'Middle Purbeck Beds' which, if accurate (and this is by no means certain), could mean an origin in either the Upper Lulworth Beds or the Lower Durlston Beds. The two specimens first described by Seeley lack even this

horizon data and are merely recorded as deriving from the Purbeck Limestone.

Until recently, the Tithonian-Berriasian boundary (and hence the Jurassic-Cretaceous boundary) was taken as the 'Cinder Bed' (now Cinder Member), partway through the 'Middle' Purbeck Limestone Formation at the boundary of the Lulworth Beds and Durlston Beds (Casey 1963, Rawson *et al.* 1978). However, Allen & Wimbledon (1991) have pointed out that current attempts to define the base of the Berriasian with more precision may alter the horizon of this boundary within the Purbeck Limestone Formation. Whereas selection of the *Subthurmannia subalpina* Subzone as the base of the Berriasian would maintain the status quo, selection of the *Berriasella jacobi* Subzone as the base of the Berriasian would shift the Tithonian-Berriasian boundary close to the base of the Purbeck Limestone Formation. Thus, at present, the pterodactyloid material discussed in this work is ambiguously Late Tithonian or Early Berriasian and is treated as such here, but should the *Berriasella jacobi* Subzone be ratified as the new base of the Berriasian, then the Purbeck Limestone Formation and its fossil assemblages would all be of Berriasian (basal Cretaceous) age.

SYSTEMATIC PALAEONTOLOGY

Order **PTEROSAURIA** Kaup, 1834
Suborder **PTERODACTYLOIDEA** Plieninger, 1901
Family **CTENOCHASMATIDAE** Nopsca, 1928

DIAGNOSIS (After Wellnhofer 1978). Pterodactyloids with elongate, anteriorly rounded snout. Food-trapping dentition composed of a large number of long, pointed, outwardly directed teeth inserted laterally in the jaw margins. The tooth-row extends back for about half the skull length.

INCLUDED GENERA. *Ctenochasma* Meyer, 1851; *Gnathosaurus* Meyer, 1834; *Huanhepterus* Dong, 1982; *Plataleorhynchus* gen. nov.

RANGE. Upper Jurassic – basal Cretaceous; Europe and China.

Genus *GNATHOSAURUS* Meyer, 1834

TYPE SPECIES. *Gnathosaurus subulatus* Meyer, 1834 from the Tithonian of Solnhofen, Bavaria, Germany.

DIAGNOSIS (After Wellnhofer 1978 with further points in parenthesis). Relatively large ctenochasmatids with long slender skulls, jaw tips spatulate and anteriorly rounded. Premaxillae bear a low sagittal crest extending from one third of the skull length behind the snout tip to the level of the orbit. Prominent dentition (30–32 teeth per ramus), extending back to the level of the anterior edge of the nasoantorbital fenestra. The anterior spatula teeth are short and anteriorly directed, the posterior spatula teeth being longer. From the 5th tooth back on each side, the teeth lengthen substantially and are anteroposteriorly directed so that each overlaps outside the tooth in front. (The posterior teeth are much shorter). Teeth are arranged to give a food-grabbing and 'fish-basket' dentition, with the teeth inserted on the lateral edge of the jaw margin and the tips inwardly directed

Naso-antorbital fenestra about twice as large as the orbit.

RANGE. Tithonian/Berriasian of Germany and England.

Gnathosaurus macrurus (Seeley) comb. nov.   Figs 1, 2

1869   *Pterodactylus macrurus* Seeley: 89–90 *partim*
1875   *Doratorhynchus validus* (Owen); Seeley: 465–8 *partim* (*non* Owen 1870)
1891   *Doratorhynchus validum* (Owen); Woods: 169 *partim* (*non* Owen 1870)
1901   *Doratorhynchus validus* (Owen); Seeley: 173 *partim* (*non* Owen 1870)
1929   *Doratorhynchus validus* (Owen); Plieninger: 27–28 *partim* (*non* Owen 1870)
1958   *Doratorhynchus validus* (Owen); Delair: 70–1 *partim* (*non* Owen 1870)
1978   *Doratorhynchus validus* (Owen); Wellnhofer: 58 *partim* (*non* Owen 1870)
1986   *Doratorhynchus validus* (Owen); Howse: 318–20 *partim* (*non* Owen 1870)

LECTOTYPE. SMC J5339, the anterior region of a mandible of a medium-sized pterodactyloid, exposed in dorsal aspect (Figs 1, 2). This specimen has not previously been figured. Seeley (1869) based '*Pterodactylus*' *macrurus* on two elements, this mandible and a cervical vertebra which thus constituted the syntypes of this species. There is no reason to associate these two specimens and the vertebra could belong to either of the large ctenochasmatids described here. Although only the vertebra has been figured previously, the mandible is more critically diagnostic of a taxon, and we have accordingly selected it as the lectotype of *macrurus*.

DIAGNOSIS. Species of *Gnathosaurus* in which the spatula on the lower jaw bears 10 teeth (14 in *G. subulatus*) and in which the main series of post-spatula mandibular teeth are nearly laterally directed (antero-laterally directed in *G. subulatus*).

TYPE LOCALITY. Quarry near Langton Matravers, Purbeck, Dorset (Seeley 1875). The precise locality is not known.

HORIZON. Purbeck Limestone Formation; Tithonian, Upper Jurassic or Berriasian, Lower Cretaceous. The precise horizon is not known.

DESCRIPTION. SMC J5339 comprises an incomplete mandible exposed in dorsal aspect (Figs 1, 2). The anterior region is abraded, the middle region is well preserved and the posterior ends of both rami are absent. The anterior regions of the mandibular rami coalesce with a long narrow common symphysis (Fig. 1). The length from the anterior tip of the mandible to the broken end of the longest ramus is 308 mm, the length of the symphysis is 122 mm, and the greatest width between the diverging rami is 51 mm. The anterior extremity of the symphysis is expanded into a small spatula about 22 mm wide and 23 mm long (Fig. 2A). This is rounded anteriorly but then narrows more gradually posteriorly to give an elongate shape. The spatula bears ten alveoli, five on each side. Their arrangement indicates that the spatula teeth were all directed anterolaterally. Behind the spatula, the symphysis constricts to a width of 12 mm, then widens to 25 mm at the point where the rami diverge. At this point, the rami meet at an acute angle and completely ankylose, there being no trace of a symphysial suture. The symphysial region is relatively shallow and does not appear to have been crushed *post-mortem*.
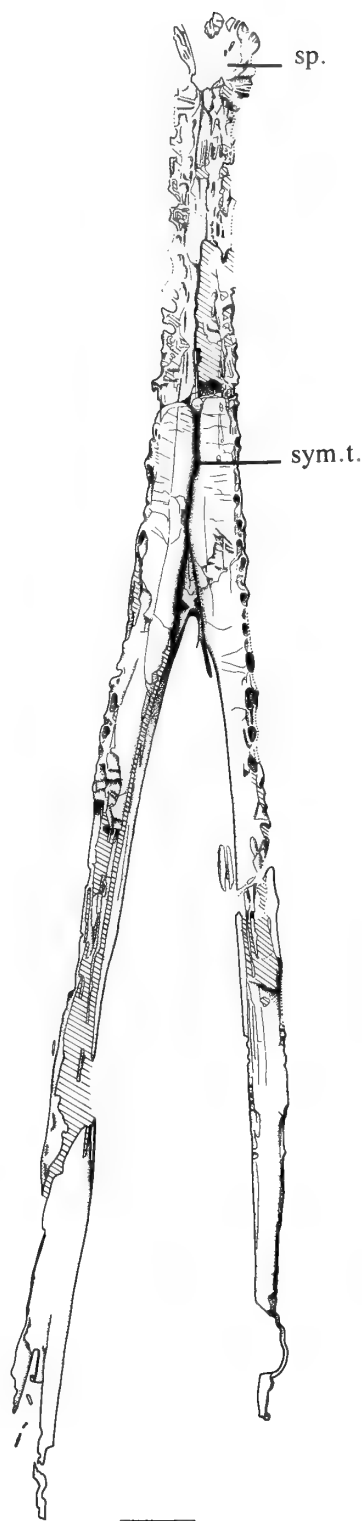
Fig. 1 *Gnathosaurus macrurus* (Seeley) comb. nov. SMC J5339, lectotype. Anterior region of mandible in dorsal aspect. Abbreviations: sp. = spatula; sym.t. = symphyseal trough. Scale = 10 mm.
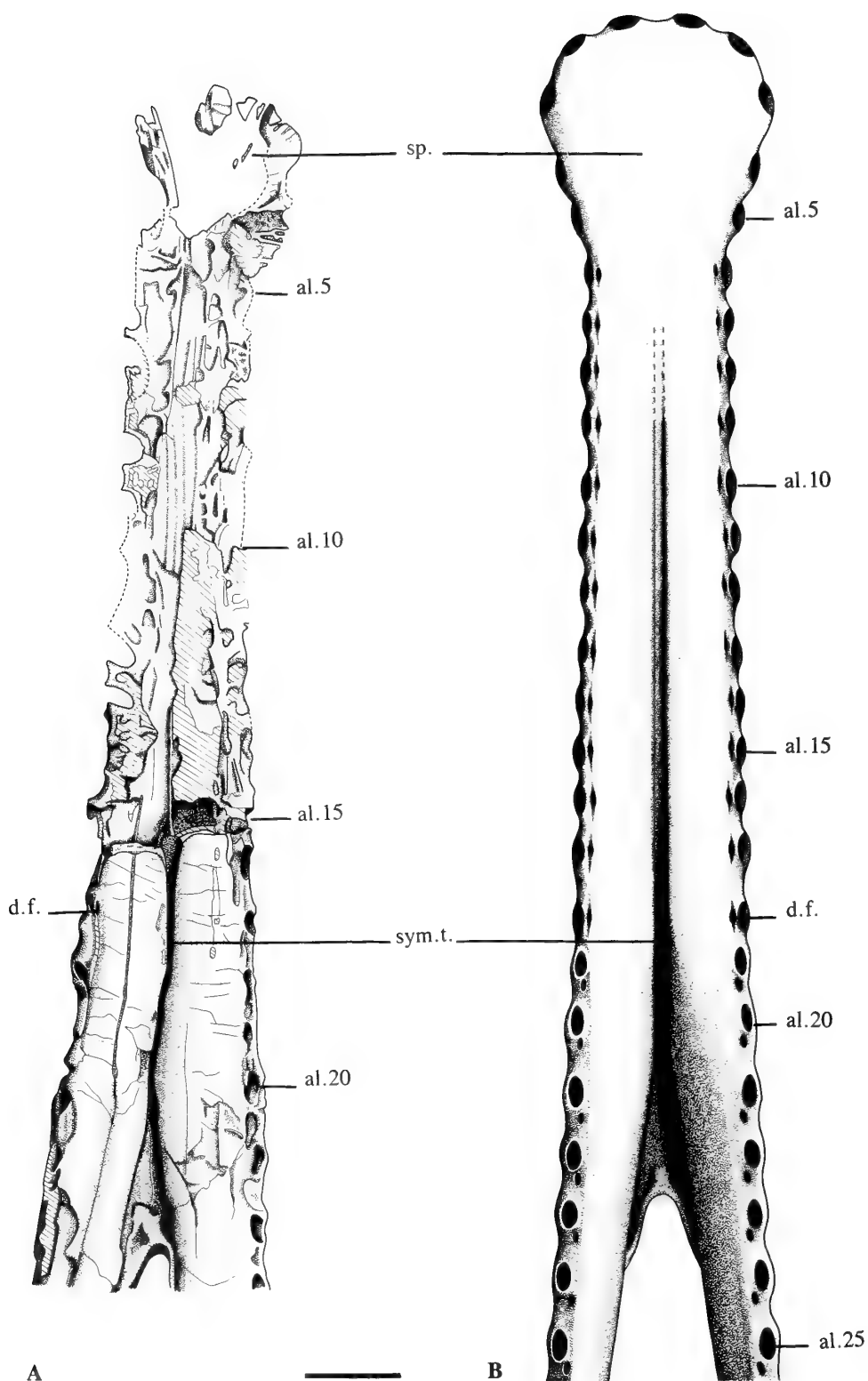
Fig. 2 *Gnathosaurus macrurus* (Seeley), comb. nov. SMC J5339, lectotype. (A) Symphyseal region as preserved. (B) Reconstruction of anterior mandible in dorsal aspect. Abbreviations: al. = alveolus; d.f. = dental foramen; sp. = spatula; sym.t. = symphyseal trough. Scale = 10 mm.

On the dorsal side of the midline of the symphysis is a symphysial trough, a groove about 2 mm wide and between 1 and 2 mm deep, with smoothly rounded edges. The trough has been slightly distorted by lateral pressure, and would have originally had the cross-section of a narrow steep-sided 'V'. The trough walls were convex in section and the floor was narrowly rounded. The trough is a narrow structure set in a relatively broad buccal floor. The trough widens over the posterior 12 mm of the symphysis, its floor becomes gently concave, and its walls merge into the ventro-medial walls of the jaw rami over the first 5 mm behind the symphysis.

A series of poorly preserved alveoli are visible on the dorsal edge of each ramus, the more complete series on the right extending back to about 50 mm behind the level of the posterior end of the symphysis. They are small and ovoid, between 1·5 and 2 mm labio-lingually and 3 mm antero-posteriorly. The alveolar rims are not raised into cylindrical collars like those of *Plataleorhynchus*, described below. Alveolus 15 on the right side is exposed in section and is deep, extending almost to the midline. Within the symphysis is a median septum of bone separating the two series of alveoli. Unlike the anterolaterally orientated spatula alveoli, those of the post-spatula region are arranged perpendicular to the midline, and the main tooth-row must have extending out sideways from the jaw. The alveoli on the spatula and anterior mandible were nearly horizontal, whereas those further back were more dorsolaterally orientated, there being a gradual gradation along the mandible. There are 29 alveoli visible on the right dentary and about 30 were probably present on each ramus (including the spatula teeth). They imply the presence of a large number of small, outwardly-directed teeth spaced evenly at approximately 3·25 mm intervals.

SYSTEMATIC POSITION. SMC J5339 is clearly the mandible of a ctenochasmatid pterodactyloid. It is shallow, has a long symphysial region and would have borne about 30 laterally or antero-laterally directed teeth of uniform cross-section on each side (Fig. 2B). The small spatula would have borne ten anterolaterally directed teeth. The buccal floor of the symphysial region has a broad flat surface curving down medially to a narrow symphysial trough. Such flattened mandibles with large numbers of evenly spaced, uniform, laterally orientated teeth are only found in the Ctenochasmatidae, although the symphysial trough appears at first to conflict with this position as it has been used as a character to define the Ornithocheiridae.

The symphysial trough has previously been reported as an ornithocheirid character (Wellnhofer 1978) but appears to have a wider distribution, although in different configurations. Ornithocheirids have either a shallow 'U'-shaped symphysial trough (*Ornithocheirus sedgwicki* and *O. daviesi*) or a wide 'V'-shaped trough (*O. machaerorhynchus* and *Brasileodactylus araripensis*). In all these forms, the buccal floor forms a narrow shelf on either side of the trough and the teeth are vertically orientated. The holotype and only mandible (BSPM AS VII 369) of the ctenochasmatid *Gnathosaurus subulatus* is preserved with ventral aspect only exposed and the presence of a trough cannot be established. However, the palate of *G. subulatus* bears a low medial ridge presumably developed from the co-ossified palatines. For the rostrum and mandibles of *G. subulatus* to occlude in a useful manner, there must have been a corresponding medial trough in the symphysial region of the mandibles of this species. The

palatal ridge, though low, is sharply keeled and narrow, and the trough in SMC J5339 is of corresponding shape for such a keel to fit into. This type of keel-trough system, in which a small sharp keel and trough occur between wide palatal and buccal shelves in flattened jaws, appears to characterise some members of the Ctenochasmatidae. Thus the presence of a symphysial trough does not characterise the Ornithocheiridae *sensu latu*, but specific constructions of trough characterise separately the Ornithocheiridae and some Ctenochasmatidae.

Within the Ctenochasmatidae, SMC J5339 is closest to *Gnathosaurus subulatus* in configuration. The presence of 30 teeth per ramus is comparable to counts of 31 in *G. subulatus* and ?36–38 in *Plataleorhynchus*, but distinct from 50–90 in *Ctenochasma* and 25 in *Huanhepterus*. The small mandibular spatula bearing 10 teeth is unlikely to have been the counterpart to the large rounded rostral spatula bearing 22 teeth found in *Plataleorhynchus* and the latter bears no medial ridge that might correspond to the upper part of the ridge-trough system in *Gnathosaurus*. In shape, the spatula of SMC J5339 is comparable to that of *G. subulatus* and the latter bears a medial ridge on the palate corresponding to the symphysial trough of the mandible of SMC J5339. It is proposed that SMC J5339 be placed in the genus *Gnathosaurus* as the species *macrurus*, distinguished from *G. subulatus* by the difference in number of spatula teeth (10 in *macrurus*, 14 in *subulatus*) and the orientation of the post-spatula teeth (lateral in *macrurus*, anterolateral in *subulatus*).

Genus *PLATALEORHYNCHUS* nov.

NAME. From the Greek: *Platalea*, the generic name of the spoonbill, derived from *Platys* – flat; and *Rynchos* (latinised to *Rhynchus*) – a snout.

TYPE SPECIES. *Plataleorhynchus streptophorodon* sp. nov.

DIAGNOSIS. As for the type and only species.

RANGE. Tithonian/Berriasian of the British Isles.

Plataleorhynchus streptophorodon sp. nov.   Figs 3–6

NAME. From the Greek: *streptophoros*, collar-wearing, and *odontos*, a tooth.

DIAGNOSIS. Large ctenochasmatid attaining a skull length of at least 400 mm, if *Gnathosaurus*-like proportions are assumed. Spatula roughly circular and relatively sharply demarcated from narrow rostrum posterior to it. Spatula bearing 22 teeth with shallow roots not reaching to the centre of the spatula. Anterior tip of palatines forming a slender point wedged between the two premaxillaries. Palatal face of spatula and anterior rostrum partly covered in rugose bone, indicative of the presence of a keratinous pad. No ridge on the midline of the palate. Over 62 (possibly up to 76) teeth present on entire rostrum.

HOLOTYPE. BMNH R.11957. Rostrum of a pterodactyloid visible in palatal aspect (Figs 3–5). *Ex* Corfe Castle Museum collection, purchased by BM(NH) from Dorset County Museum in 1958. Not previously described.

TYPE LOCALITY. Quarry near Langton Matravers, Purbeck, Dorset. The precise locality is not known.

HORIZON. 'Middle Purbeck Beds', Purbeck Limestone For-

mation; Tithonian, Upper Jurassic or Berriasian, Lower Cretaceous. The precise horizon is not known.

DESCRIPTION. BMNH R.11957 is an incomplete section of a pterodactyloid rostrum, 174 mm long, exposed in palatal aspect, and comprising the premaxillaries, maxillaries and palatines (Figs 3, 4A). These elements are partly fused and only some sutures can be identified.

Spatula. The rostrum bears a terminal spatula which is completely flat and shows no longitudinal or transverse curvature (Fig. 5). It is formed by the premaxillaries which are completely fused in the midline. It is 39 mm long and 32 mm wide and bears 22 alveoli around its periphery. The anterior alveoli are damaged and represented by the broken edges of the bases. The remaining alveoli on the spatula are better preserved although the rims are never complete. The spatula alveoli are between 0·75 and 1·25 mm apart and all but the anterior pair are between 3·5 and 3·75 mm wide labiolingually, the anterior pair being about half this size. The alveoli in the anterior half of the spatula are anteriorly or anterolaterally orientated, those in the posterior half gradually becoming more laterally orientated. The posteriormost spatula teeth would have emerged posterolaterally from the spatula, in sharp contrast to the anterior post-spatula teeth which would have been laterally directed. In all cases, the teeth would have emerged horizontally from the edges of the jaws. The alveolar rims are formed from short raised collars of bone, which tend to coalesce with neighbouring rims on the spatula, giving it a slightly crenellated margin. Radiography of the spatula has shown that the tooth sockets within it are short and extend only partway to the middle of the spatula. Although the teeth are missing, the small size of the sockets suggests that the teeth themselves were not large or required to cope with powerful movements of prey animals.

The palatal surface of the spatula is perforated by an outer and an inner series of foramina (Fig. 5). The outer series occurs in two parallel rows of elliptical foramina close to the alveolar bases along the rostrum and forms a loop of 23 small circular openings on the spatula. This series bears a one-to-one relationship to the 22 alveoli (except for the third alveolus on the left side which has 2) and the openings are presumed to be the dental foramina. Each dental foramen is set 4–5 mm in from the nearest tooth. The inner series of foramina are larger, fewer in number (ten on the spatula) and

more variable in shape. They are asymmetrically arranged with three on the left side and seven on the right side. Several emerge into shallow channels on the surface of the palate. One pair of inner foramina at the 'neck' of the spatula develop into diverging anterolaterally directed channels, while the anterior pair of foramina on the spatula each develop into forked anterolaterally directed channels separated by a V-shaped notch.

The centre of the palatal surface of the spatula is covered by a pad of rugose bone which puts out local anterolateral extensions to the periphery of the spatula (Fig. 5). Posteriorly the rugose patch becomes elongate and, at the level of the 'neck' of the spatula, it is flanked by two other elongate but irregular rugose zones. Patches of rugose bone are also present around and near the bases of the alveoli. The surface of the central rugosity consists of a dense pattern of ovoid cancellations separated by minute spans of bone. Near the periphery of the spatula these cancellations become circular pits. The non-rugose parts of the spatula are only lightly pitted, as are the outer alveolar walls and most of the palatal surface of the elongate region of the rostrum.

Post-spatula rostrum. Behind the spatula, the rostrum narrows to 15 mm in width and then gradually broadens (Figs 3, 4A). The premaxillaries extend back behind the spatula for a further 36 mm but here the medial suture is still present. Behind the premaxillaries are the fused palatines in the midline and the paired maxillaries on either side. The palatines terminate in a narrow point anteriorly and are slightly sloping to give a raised midline to the palate. The maxillary-palatine sutures are largely visible, except where damaged, but the premaxillary-maxillary sutures cannot be seen clearly. The posterior palatal shelf of each maxillary bears a long shallow trough between the alveoli and the suture with the palatine. These troughs fade out well behind the spatula. The damage to the rostrum appears to involve some anteroposterior compression or telescoping with some anteroposterior overlap of elements. The reconstruction of the rostrum (Fig. 4B) attempts to compensate for this compression, assumed to be equivalent to the space occupied by 3–4 teeth on each side.

There were at least 20 post-spatula teeth on each side and, if it is assumed that some telescoping of the rostrum has occurred and that a few more teeth were present posteriorly,
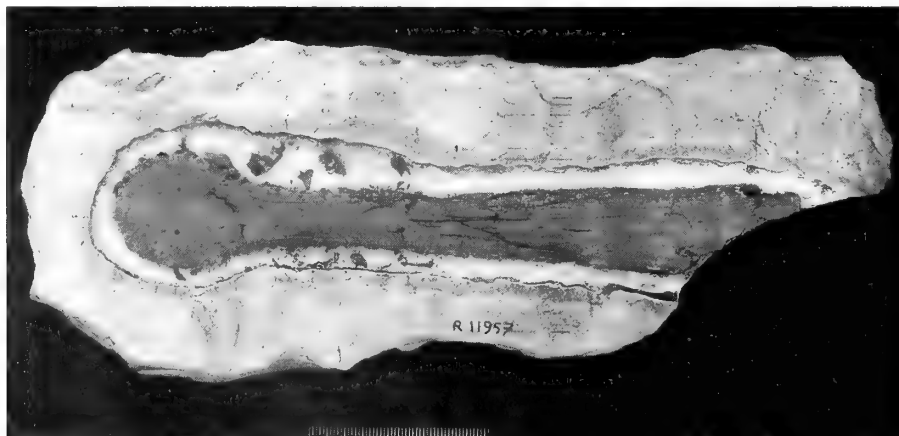
Fig. 3   *Plataleorhynchus streptophorodon* gen. et sp. nov. BMNH R.11957, holotype rostrum in palatal aspect x 0·7.
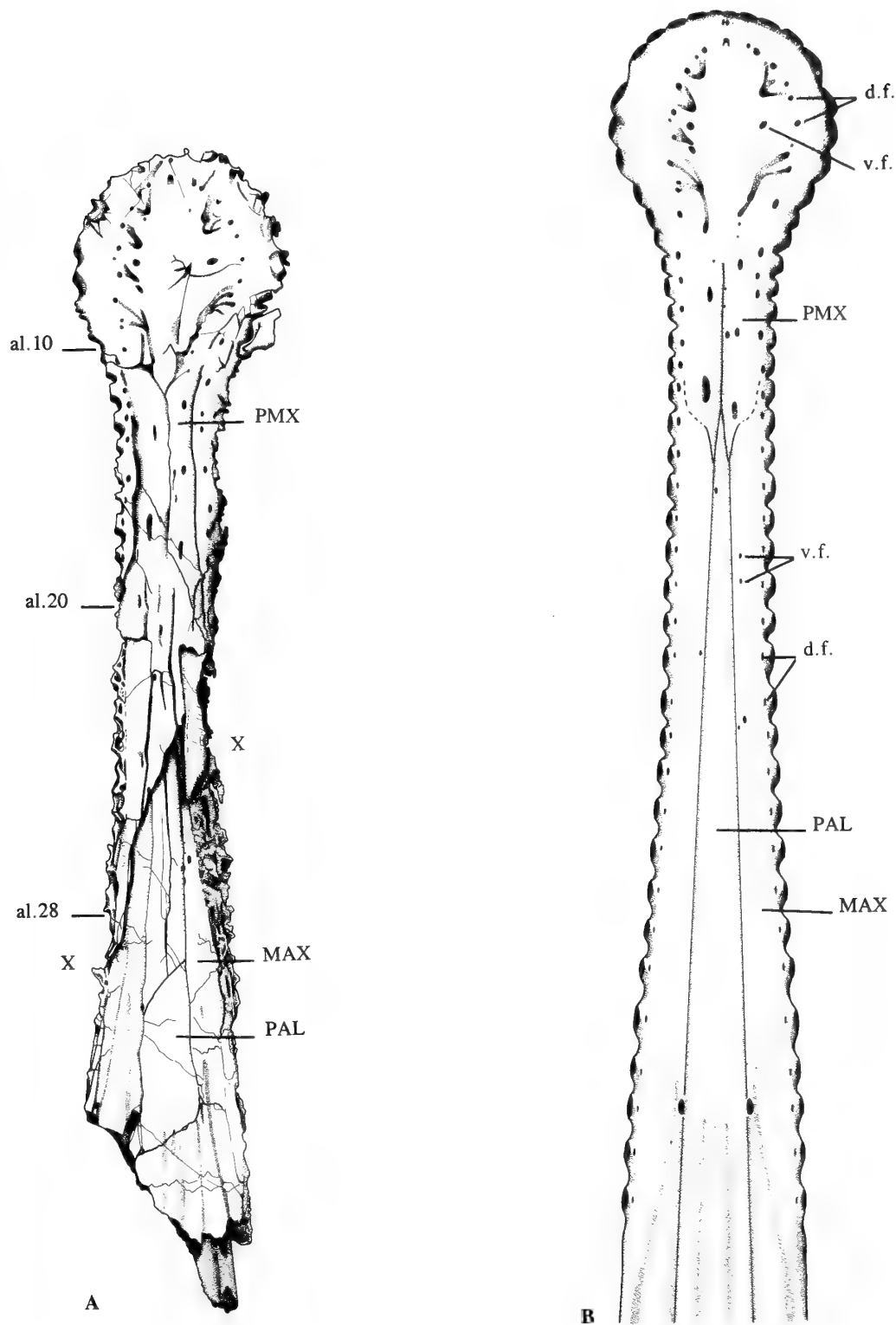
g. 4 *Plataleorhynchus streptophorodon* gen. et sp. nov. BMNH R.11957, holotype rostrum in palatal aspect. (A) Interpretive drawing. (B) Reconstruction of rostrum. The reconstruction incorporates compensation for the telescoping of the original specimen, and is therefore somewhat longer. Abbreviations: al. = alveolus; d.f. = dental foramen; MAX = Maxillary; PAL = Palatine; PMX = Premaxillary; v.f. = vascular foramen; x–x crack marking region of telescoping of specimen. Scale = 10 mm.

there might have been 5–7 more in each row (Fig. 4B reconstruction). Their alveoli are similar in size to those of the spatula teeth, but are less closely spaced with 2·5 to 3·5 mm separation, and their 'collars' show no tendency to coalesce. The dental foramina move to close proximity to the teeth behind the spatula and are incorporated into the base of the alveolar rim by tooth 17 on each side. On either side of the midline of the post-spatula rostrum are a series of large oval foramina, corresponding to the inner foramina on the spatula. Most of the palatal surface in this region is covered in delicate anteroposteriorly orientated striae, with occasional rugose patches along the midline. *The rugose palate surface.* In several groups of vertebrates, notably chelonians, birds and some ornithischian dinosaurs, the presence of a horny beak or palate is associated with a characteristic rugose surface to the bone underlying the horn-covered area. This is noticeable in the palates of many living turtles and birds, where the association between the horny beak and crushing palate and the rugose and vascular underlying bone is indisputable. Such palatal surfaces have not been previously reported in tooth-bearing pterosaurs, but are present in *Plataleorhynchus* as described here. A search through specimens available to us has revealed a slender strip of rugose bone on the anterior palate of the anhanguerid 'Ornithocheirus' cuvieri from the Lower Chalk of Kent (pers. obs.) and it is likely that such structures were present in other large pterodactyloids at least. It appears that *Plataleorhynchus* had a pad of horny skin on the palatal surface of the spatula and along parts of the anterior palatal surface of the rostrum. Such horny palatal surfaces generally occur where a hard renewable surface is required by a feeding technique involving crushing or abrasion, which would cause damage to a surface that was not both hard and self-regenerating.

SYSTEMATIC POSITION. The only pterosaurs to have a rostrum with such a pronounced flat spatula and slender, laterally directed teeth are some members of the family Ctenochasmatidae, also known from the Upper Jurassic of Europe and China. *Plataleorhynchus* can be distinguished from each of the three previously described ctenochasmatids as follows:

Ctenochasma Meyer, 1851, represented by three species from Germany and France, is the type genus of the family. It is known only from relatively small specimens, lacks a spatula and has a much larger number of closely spaced teeth (100–180) in the upper jaw. Although the only rostrum of *Plataleorhynchus* is incomplete and the full rostral tooth count is unknown, it is unlikely to be much greater than 76.

Huanhepterus Dong, 1982, represented by the single species *H. quingyangensis* from China, is of suitable size, has a terminal expansion to the rostrum but is estimated to have a rostral tooth count of about 50, significantly fewer than the other ctenochasmatid genera including *Plataleorhynchus*.

Gnathosaurus Meyer, 1834, represented by *G. subulatus* from Germany and *G. macrurus* from Purbeck has a similar number of rostral teeth to *Plataleorhynchus*, but the spatula is less circular, more ovoid in ventral aspect, bears only 10–14 teeth, and the tooth orientation change between the posterior spatula dentition and the anterior post-spatula dentition is gradual. The anterior region of the spatula bears very large teeth, the roots of which extend into the middle of the spatula. There is no evidence of rugosity on the palatal

surface of the spatula or rostrum. In *Plataleorhynchus*, the spatula is almost circular in plan view, bears 22 teeth and the alveoli show a very sharp demarcation in orientation at the spatula-postspatula boundary. The anterior marginal teeth of the spatula do not appear to have been large and their sockets extend only partway towards the middle of the spatula. The palatal face of the spatula and anterior rostrum are partly rugose, as described above.

Plataleorhynchus is closest to *Gnathosaurus* in general configuration but is larger and has a rostrum showing greater differentiation between the spatula and post-spatula areas. In conclusion, *Plataleorhynchus* can be argued to represent a new genus of large ctenochasmatid with a large spoonbill-like rostrum.

LIFE STYLE. Most ctenochasmatids appear to have been filter-feeders, the long rostrum bearing long laterally directed, intermeshing teeth, providing a sieve-like device for filtering small crustaceans or similar organisms from the water or mud. *Plataleorhynchus* may likewise have been a sweep-feeder like the living spoonbill *Platalea*, swinging the head from side to side and filter feeding on a large scale. It is possible that *Plataleorhynchus* may have fed in a slightly different manner, in that, compared to other large ctenochasmatids, the terminal spatula was more differentiated, the teeth were relatively smaller (to judge from the alveoli) and the palatal surface appears to have been covered by a horny surface (Fig. 6). These suggest that the animal may have used its spatula and anterior dentition to rake through mud or weed to disturb animals, then gripping and crushing slightly larger animals in the water or substratum with the horny spatula as they were disturbed. This may have been a more significant means of procuring food for this large ctenochasmatid than simply filtering water with organisms in it.

CTENOCHASMATIDAE *Incertae sedis*

CERVICAL VERTEBRAE. SMC J5340 is a middle series cervical vertebra of a pterodactyloid, exposed in dorsal aspect and dorso-ventrally crushed. The specimen was figured by Seeley (1875 fig.1 (unnumbered), 1901 fig.65) and Howse (1986 figs 8–9). It came from near Langton Matravers, Purbeck, Dorset (Seeley 1875) and probably from the same horizon as the lectotype of *Gnathosaurus macrurus*. The precise locality is not known.

SMC J5340 is either a fourth or, more probably, a fifth cervical vertebra of a long-necked pterodactyloid. It was most recently redescribed by Howse (1986) and the following is a brief summary of that description. The specimen has been crushed in a generally dorso-ventral plane with some lateral distortion, so that the apex of the neural arch has been displaced to the left of the centrum midline. The centrum is 109 mm long, but is largely obscured by the neural arch. The anterior cotyle and posterior condyle of the centrum are too crushed for much of their structure to be made out, although the posterior condyle was situated between a pair of postexapophyses, the left one of which is preserved. There is a small oval pneumatic foramen about halfway along the centrum, visible on the exposed right side.

The neural arch appears to have been a low-vaulted, somewhat rounded structure. It is broad-ended, tapering to a narrow waist about two-thirds of its length from the anterior. The anterior margins of the neural arch were extended into
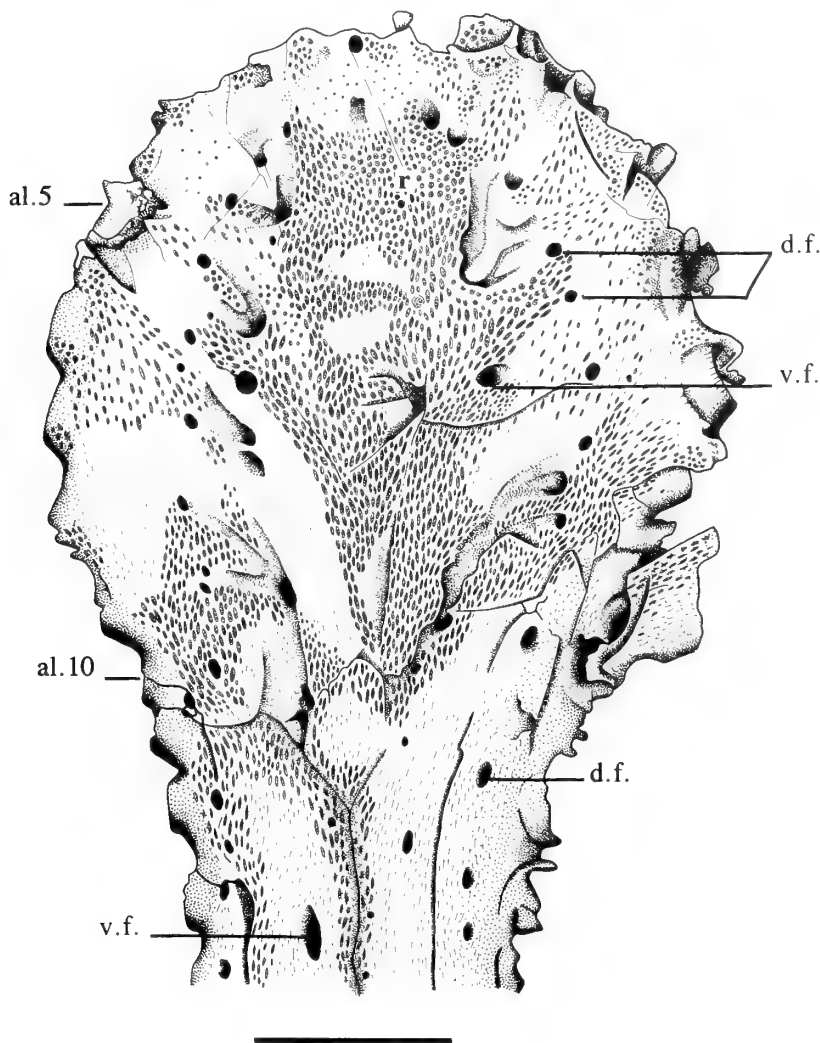
Fig. 5 *Plataleorhynchus streptophorodon* gen. et sp. nov. BMNH R.11957, spatula of rostrum in palatal aspect (interpretive drawing). Abbreviations: al. = alveolus; d.f. = dental foramen; v.f. = vascular foramen. Scale = 10 mm.

parallel, elongate, horn-like prezygapophyses, the left one of which is preserved. It bears an ovoid articular facet. The postzygapophyses, represented by a worn left structure, were broad blunt processes each bearing a distinct tubercle. The neural spine is a low slender ridge of bone running the full length of the vertebra. Fracturing at both ends suggests that it may have been slightly more raised in these regions.

BMNH 48387 (Fig. 7) is a second, incomplete, cervical vertebra which is part of the Beckles Collection, purchased in 1877. It is recorded merely as having been collected from the 'Middle Purbeck Beds' of Durlston Bay. It is a fragment comprising the posterior end of a flattened and elongate cervical vertebra similar to the above specimen. Like SMC J5340, it has a low neural spine and bears a pair of postexapophyses which bracket the posterior condyle.

These elongate cervical vertebrae clearly do not belong to an ornithocheirid, a gallodactylid or some pterodactylids. Such vertebrae are found in the Ctenochasmatidae, the Azhdarchidae and some species of *Pterodactylus*, including *P. antiquus* and *P. longicollum* (the latter two possibly

synonymous according to Bennett (1993)). In recent work SMC J5340 has been treated as a fragment of a possible early azhdarchid pterodactyloid (Howse 1986, Wellnhofer 1991a). However, now that it has been established that two suitably large ctenochasmatids, *Plataleorhynchus* and *Gnathosaurus*, are present in the Purbeck Limestone Formation, the systematic position of this cervical must be reconsidered. The larger ctenochasmatid *Huanhepterus* has cervicals of similar size and proportion and this size and shape of cervical vertebra could reasonably be predicted to be present in *Plataleorhynchus*. Nevertheless, given the diversity of long-necked forms in the slightly earlier pterodactyloid fauna from the Solnhofen Limestone, such a cervical cannot be confidently assigned to a particular genus, and it is here treated as indeterminate ctenochasmatid material.
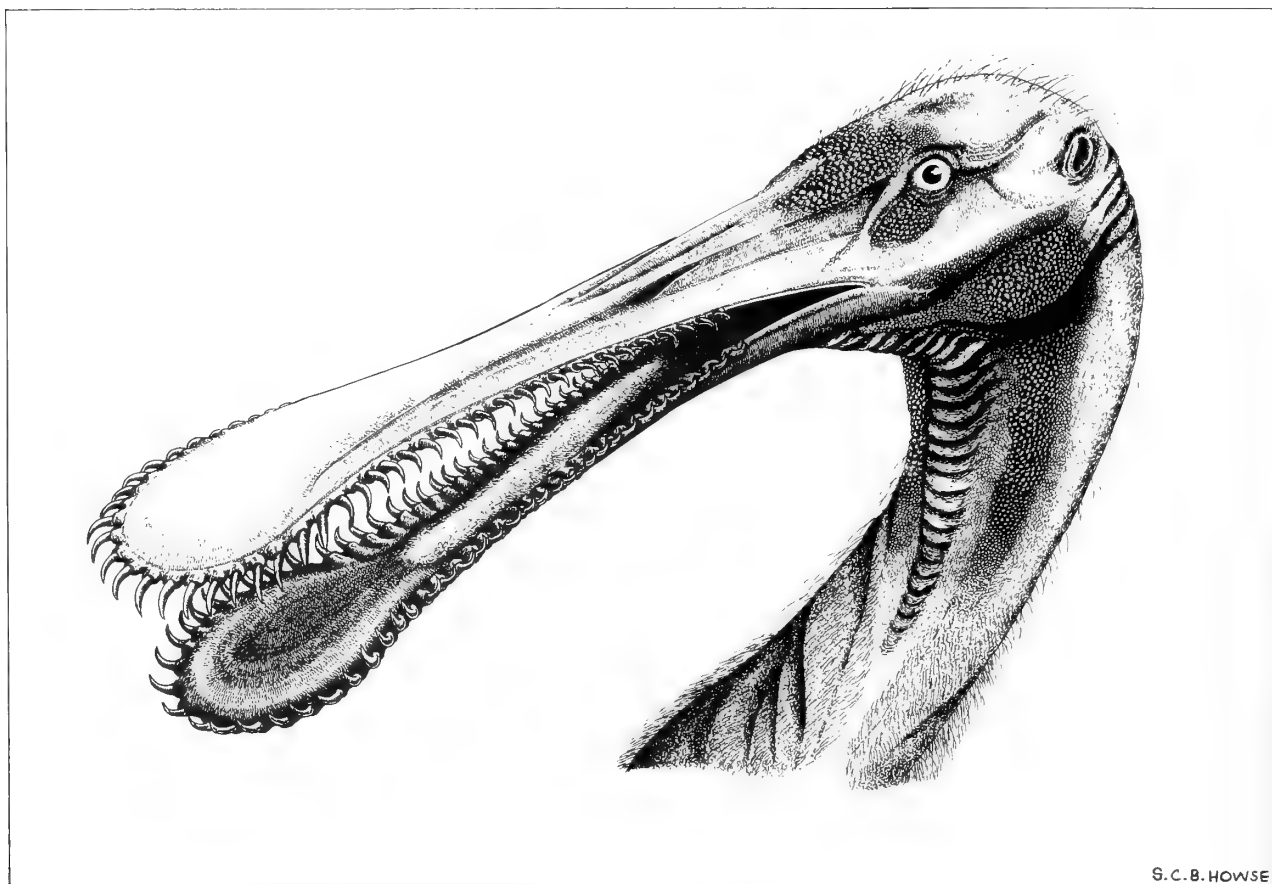
Fig. 6 Restoration of the head of *Plataleorhynchus streptophorodon*, to show relationship of spatula to the head, using the ctenochasmatids *Gnathosaurus* and *Ctenochasma* as models.
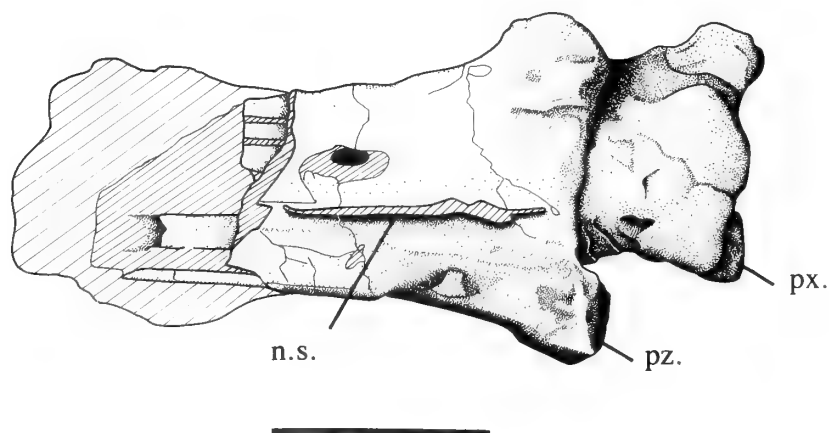
Fig. 7 Incomplete indeterminate ctenochasmatid cervical vertebra. BMNH 48387. Abbreviations: n.s. = neural spine; px. = postexapophysis; pz. = postzygapophysis. Scale = 10 mm.

Family **ORNITHOCHEIRIDAE** Seeley, 1870

SYSTEMATIC NOTE. Bennett (1989) has proposed uniting a range of advanced pterodactyloids including the ornithocheirids, pteranodontids and '*Ornithodesmus*' in one family under the name Pteranodontidae Marsh, 1876. In this work, we follow the practice of Wellnhofer (1991b) in dividing these forms into several families, pending a more comprehensive analysis of their relationships.

Genus *ORNITHOCHEIRUS* Seeley, 1869

TYPE SPECIES. *Ornithocheirus compressirostris* (Owen) Seeley: from the Turonian of Burham, Kent, England (see Wellnhofer 1978 pp. 55–56 for discussion of the identity of the type species of *Ornithocheirus*).

'*Ornithocheirus*' sp. A   Fig. 8

MATERIAL. BMNH R.11958, the anterior region of a mandible of a pterodactyloid exposed in ventral aspect (Fig. 8). The specimen is somewhat crushed and the teeth have all been lost. *Ex* Corfe Castle Museum collection, purchased by BM(NH) from Dorset County Museum in 1958.

TYPE LOCALITY. 'Near Swanage', Dorset. The precise locality is not known.

HORIZON. 'Middle Purbeck Beds', Purbeck Limestone Formation; Tithonian, Upper Jurassic or Berriasian, Lower Cretaceous. The precise horizon is not known.

DESCRIPTION. BMNH R.11958 comprises the anterior region of a pterodactyloid mandible exposed in ventral aspect on a block of limestone (Fig. 8). It consists of a complete elongate symphysial region and posteriorly incomplete rami, the length of the incomplete specimen being 208 mm in the midline. The symphysial region is 118 mm long and relatively narrow, passing from 9 mm width near the tip, to 20 mm width where the rami diverge. There is a slight spatulate expansion of the tip. A short section of the symphysis is visible in dorsal aspect and shows the presence of a median trough with a deep 'V'-shaped cross-section, and a few oval alveoli. The buccal shelves on either side of the trough are relatively narrow.

Most of the alveoli of the symphysial region cannot be observed directly although their lateral edges can be seen as undulations along the jaw margin, at least demonstrating that teeth were present in this region. The few alveoli visible appear to be widely spaced at intervals of about 6 mm. If this is uniform, there would be space for about 23 on each ramus. The ventral midline of the symphysial region bears a distinctive low keel. For the first 26 mm of its length, the symphysis is a flattened structure and the keel, which originates 9 mm behind the tip, is a low slender ridge about a millimetre wide and with a semicircular cross-section. For the next 35 mm, the symphysial region becomes a deeper, steeper-sided structure and the keel is a deeper ridge with a V-section merging into the sides of the mandible. For the posterior 56 mm of its length, the symphysial region is severely crushed, but the more resistant keel has resisted the crushing and forms a sharp crest extending to the back of the symphysis.

The rami are crushed outwards so that their width of 5–6 mm represents their original depth. A consequence of this crushing is that the dorsal edges face laterally and it can be
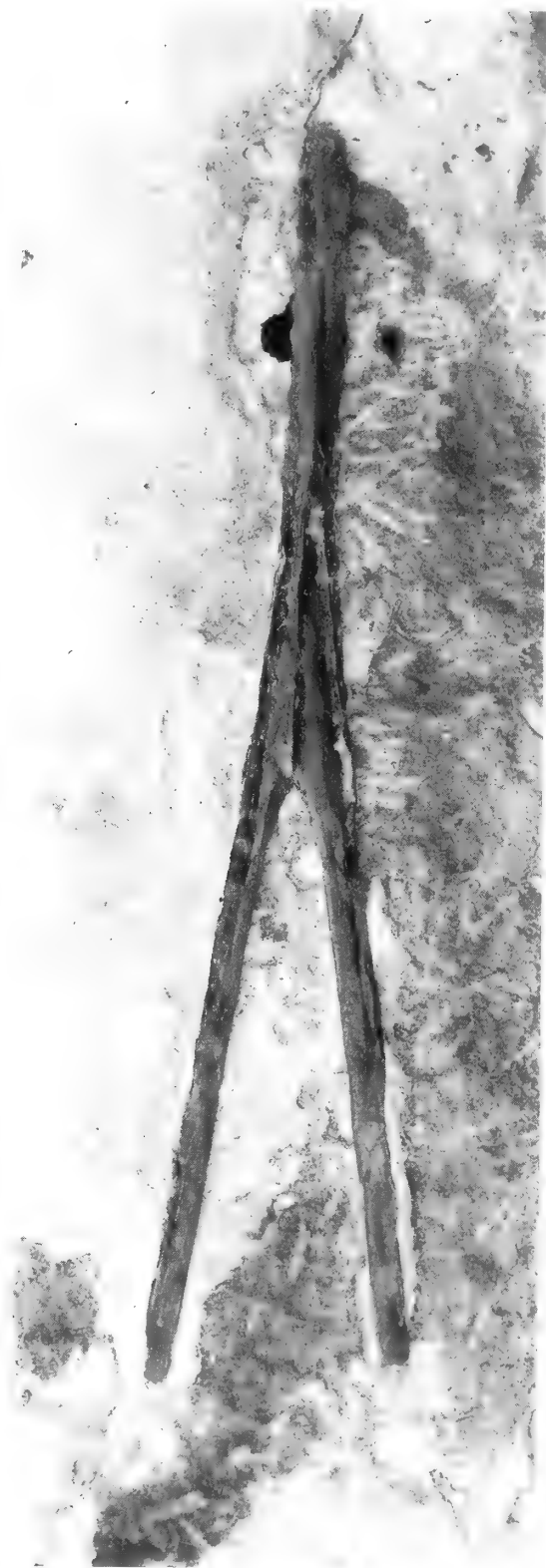
Fig. 8 '*Ornithocheirus*' species A. BMNH R.11958, anterior region of mandible in ventral aspect x 0·8.

seen that there are no alveoli behind the level of the symphysis. Crushing has splayed the rami slightly and they probably diverged less in life. The rami are broken posteriorly, anterior to the position of the articulars.

SYSTEMATIC POSITION. The discovery and description of a series of ornithocheirids, criorhynchids and anhanguerids from the Santana Formation of Brazil has resulted in the systematics of this group passing though a period of instability while new relationships and systematic criteria are defined. The Ornithocheiridae as used in recent years appears to be defined on negative criteria, and represents those members of the old Ornithocheiridae which lack the cranial outgrowths of the criorhynchids and anhanguerids. The pterodactyloid mandible described above exhibits two systematically significant characters, namely the presence of a 'V'-shaped trough extending along the midline of a symphysis, and relatively widely spaced oval alveoli. The only genera possessing these features, and an associated palatal ridge, are those until recently placed in the Ornithocheiridae *sensu latu*, but now distributed among several closely related families including the Criorhynchidae and the Anhangueridae (see Wellnhofer 1991b for a review of the taxonomy of the Brazilian members of this group). The palatal ridge and symphysial trough are known only in the Ornithocheiridae and Ctenochasmatidae and have not been described in any other Jurassic pterodactyloids, nor in *Dsungaripterus*, *Ornithodesmus*, *Noripterus*, *Pteranodon* or *Nyctosaurus*.

In the following systematic discussion, comparison is made with mandibular material of the following (sources quoted in parenthesis):

Ornithocheiridae Seeley, 1870:
    '*Ornithocheirus*' [Cambridge Greensand] (personal observation)
    Brasileodactylus [Santana Formation] (Kellner 1984).
Anhangueridae Campos and Kellner 1985:
    Anhanguera [Santana Formation] (Wellnhofer 1991b)
Criorhynchidae Wellnhofer 1991b:
    Tropeognathus [Santana Formation] (Wellnhofer 1987).

Ornithocheirus species A, represented by BMNH R.11958, has a very slight spatulate expansion, a long parallel-sided symphysis bearing a deep 'V'-shaped symphysial trough, a very low ventral V-section keel and a complete absence of ventral blades or crests. The Anhangueridae are characterized by blades and crests on the rostrum and mandible and the mandible bears a shallow 'U'-shaped symphysial trough. BMNH R.11958 is therefore not an anhanguerid. The Criorhynchidae are characterized by a massive blade of bone on the anteroventral end of the mandible and it is therefore not a criorhynchid, although the 'V'-shaped symphysial trough does occur in that family. The Ornithocheiridae is at present a residue comprising the crestless members of the old Ornithocheiridae *sensu latu*. Within the Ornithocheiridae, BMNH R.11958 most closely resembles some of the mandibular material from the Cambridge Greensand. The taxonomic status of this material has not yet been rationalized with respect to the Santana Formation pterodactyloids (that work is being undertaken by Dr D. Unwin, University of Bristol), and therefore the nomenclature of Seeley and Hooley is used in the following discussion. The Greensand specimen that most closely resembles BMNH R.11958 is the type of *Ornithocheirus machaerorhynchus* Seeley, 1870 (pl.xii, figs 1, 2), a fragment from the distal region of a mandibular symphysis
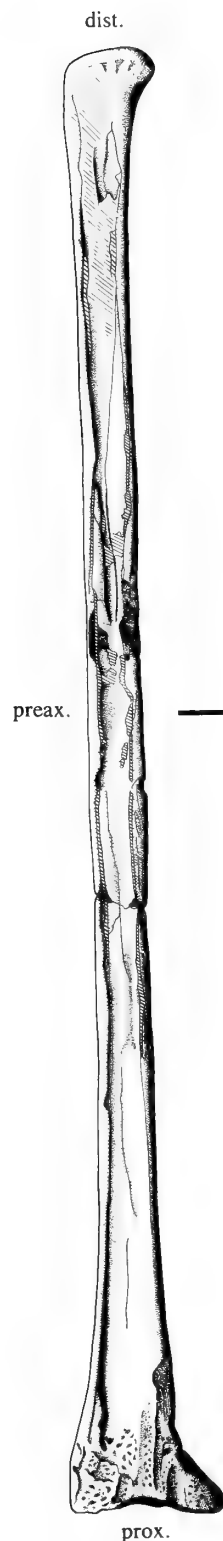
Fig. 9 *Doratorhynchus validus* (Owen) Seeley, *nomen vanum*. BMNH 40653, holotype phalanx of digit IV of right manus. Abbreviations: dist. = distal; preax. = preaxial; prox. = proximal. Scale = 10 mm.

broken at both ends. The specimen is derived from a deep symphysial region, acutely triangular in cross-section and with a ventral keel. The alveoli are oval in cross section and evenly spaced. The buccal shelves on either side of the symphysial trough are narrow, and the trough itself is deep and 'V'-shaped in cross section. No other mandibular material from the Cambridge Greensand has precisely this cross-section, but some rostral fragments bear a 'V'-shaped medial ridge on the palatal surface which appears to complement the trough in *O. machaerorhynchus*. Figured examples of such rostral fragments are the type specimens of *O. denticulatus* Seeley, 1870 (pl.xii, figs 8–9) and *O. microdon* Seeley, 1870 (pl.xii figs 6–7). Other comparable specimens described by Seeley (1870) but not figured include the type rostral fragments of *O. polyodon*, *O. nasutus*, *O. dentatus*, *O. oweni* and *O. tenuirostris*. Three specimens, the types of *O. machaerorhynchus*, *O. oweni* and *O. tenuirostris* were transferred by Hooley (1914) to the genus *Lonchodectes* while the rest were retained in *Ornithocheirus*.

Other Greensand and Chalk 'ornithocheirids' including *O. daviesi*, *O. sedgwicki*, *O. cuvieri*, *O. scaphorhynchus*, *O. platysomus* and *O. brachyrhinus*, have a shallow palatal ridge and a shallow 'U'-shaped glossal trough, quite distinct from those described above. The shallow type of trough also occurs in the Anhangueridae (but not the Criorhynchidae) and it is possible that this suite of specimens are anhanguerids.

BMNH R.11958 is significant because of its early age, but is not amenable to precise systematic placement. The absence of crests and other outgrowths, the widely spaced vertical teeth and the shape of the symphysial trough all permit it to be associated with certain of the Greensand *Ornithocheirus* 'species' of Seeley, all of which were placed by Hooley (1914) in either *Ornithocheirus* or *Lonchodectes*. It thus appears to be a member of the Ornithocheiridae *sensu stricto* and not an anhanguerid or a criorhynchid. It must be attributed to *Ornithocheirus* pending a satisfactory resolution of the systematics of that genus. Most of the named species already in the literature which incorporate or are based on comparable elements are *nomina vana* restricted to type specimens which are mandibular fragments (e.g. '*O.*' *machaerorhynchus*). In the absence of any unique diagnostic characteristics, BMNH R.11958 cannot be the basis of a new species despite its distinct stratigraphical position, and it would be misleading to refer it to *O. machaerorhynchus* on the basis of the limited similarity of mandibular fragments. Pending revision of the Greensand material, the simplest and most justifiable procedure is to record the specimen as *Ornithocheirus* 'species A'.

PTERODACTYLOIDEA *Incertae sedis*

Doratorhynchus validus (Owen) Seeley *nomen vanum*   Fig. 9

1870   *Pterodactylus validus* Owen: pl.XIX, fig.7.
1875   *Doratorhynchus validus* (Owen) Seeley: 465–8 *partim*.
1888   *Ornithochirus validus* (Owen) Lydekker: 26–7.
1890   *Doratorhynchus validus* (Owen); Woodward & Sherborn: 227 *partim*.
1929   *Doratorhynchus validus* (Owen); Plieninger: 27–28 *partim*.
1958   *Ornithocheirus validus* (Owen); Delair: 71–2.
1978   *Doratorhynchus validus* (Owen); Wellnhofer: 58 *partim*.
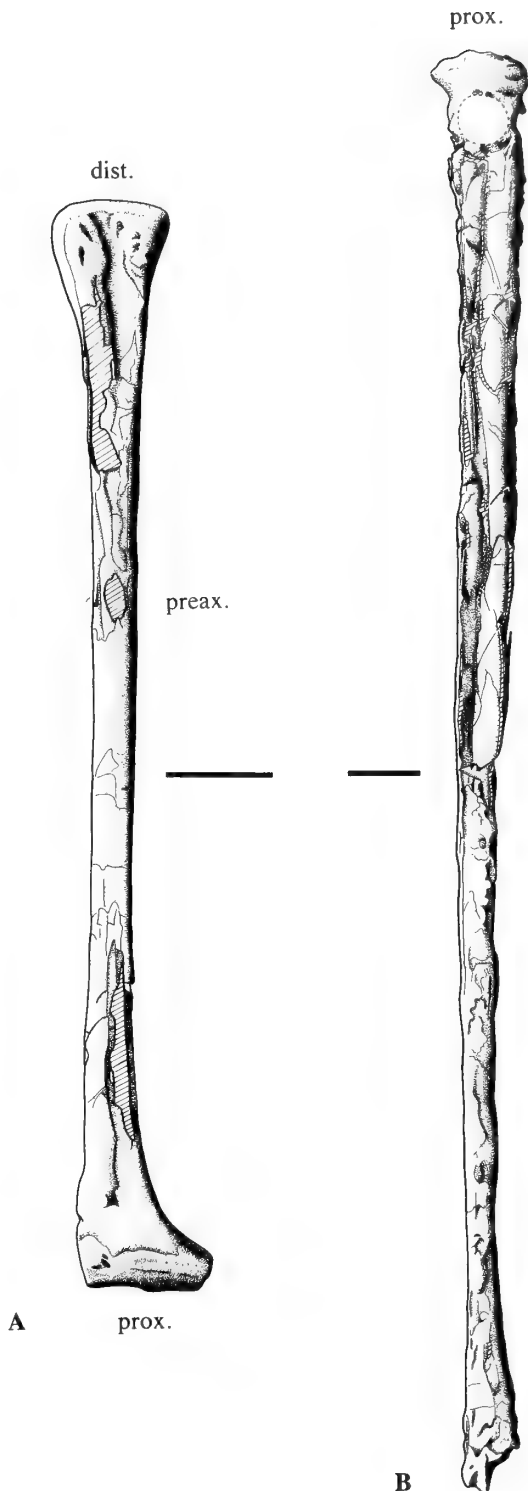
Fig. 10   Pterodactyloidea *incertae sedis*. A) BMNH 2462 right radius in ventral aspect. B) BMNH R.5798 left tibia in posterior aspect. Abbreviations as for figure 9. Scale bars = 10 mm.

The above synonymy is restricted to publications which make specific reference to the holotype phalanx.

HOLOTYPE. BMNH 40653, a first or second phalanx of digit IV (the wing-finger) of the right manus of a large pterodactyloid (Fig. 9). The specimen is exposed in dorsal aspect and was figured previously by Owen (1870 Pl.XIX, fig.7).

LOCALITY. Simply noted by Owen 1870 as 'Swanage', but probably from the Langton Matravers quarry.

HORIZON. 'Middle Purbeck Beds', Purbeck Limestone Formation; Tithonian, Upper Jurassic or Berriasian, Lower Cretaceous.

DESCRIPTION. BMNH 40653 is a crushed phalanx of digit IV (the wing-finger) of a pterodactyloid (Fig. 9). It is about 300 mm in length, with the proximal epiphysis 31 mm across and the distal epiphysis 19 mm across. There is one transverse fracture near the middle of the shaft and some superficial longitudinal fractures. The leading edge of the phalanx is straight, while the trailing edge is largely straight but curves back at each end into the posterior margins of the epiphyses. The exposed face of the bone appears to have been flat, prior to crushing, rather than of convex section, and thus probably represents the dorsal face of the phalanx. If so this was a phalanx of the right manus. The specimen was identified by Owen as the second phalanx of digit IV, and if so, would have been part of a wing finger of 1·2–1·5 metres in length. The size and extent of curvature of the distal end indicate that it was either a first or second phalanx. The shape of the proximal end resembles that of a first phalanx with the extensor process broken off. The specimen could be either a first or second phalanx of digit IV and is clearly not determinate below subordinal level. Thus the binomen *Doratorhynchus validus* is a *nomen vanum* restricted to the type specimen and no other Purbeck material can be referred to it, particularly as there are clearly at least three pterodactyloids in this assemblage.

OTHER PTERODACTYLOID MATERIAL FROM PURBECK

The following anatomically determinate pterodactyloid specimens have also been collected from the Purbeck Limestone Formation. One was recorded in Lydekker's (1888) catalogue, but several have not been mentioned in the literature.

TEETH. Ensom, Evans & Milner (1991) have reported a new microvertebrate assemblage from Sunnydown Quarry, Suttle's Quarry and other localities near Langton Matravers, Purbeck. This material includes several slender recurved pterosaur teeth (DORCM), which Ensom *et al.* identified as rhamphorhynchoid teeth, assuming them to represent the anterior fish-spearing teeth of small rhamphorhynchoids. An alternative interpretation is that they are the slender recurved marginal teeth of a large ctenochasmatid such as *Gnathosaurus* or *Plataleorhynchus*. This cannot yet be demonstrated as no intact teeth have been found with either specimen, but this would represent the most conservative interpretation of the systematic position of these teeth.

RADIUS. BMNH 2462 (Fig. 10A) is a small pterodactyloid radius from 'the Middle Purbeck of Swanage', originally in the G. A. Mantell Collection and acquired by the BM(NH) in 1838. It was listed as a phalanx by Lydekker (1888 p.27), mentioned by Wellnhofer (1978) and first identified as a radius in 1988 by S.C. Bennett (Kansas) during study of the BM(NH) collections. The radius appears to be a right element exposed in ventral aspect. It is 111 mm long, 13 mm across the proximal epiphysis, 11 mm across the distal epiphysis and 4 mm across the diaphysis at its narrowest diameter. Beyond being recognisable as a pterodactyloid radius, it is indeterminate.

METACARPAL. BMNH 48380 (Fig. 11) is a fourth metacarpal of a medium-size pterodactyloid. It formed part of the S. H. Beckles Collection and is recorded as being from the 'Middle Purbeck Beds' of Durlston Bay. It is incomplete, lacking the proximal end, but the distal end and the main shaft are about 44 mm in length, and the entire bone would have been 50–55 mm long. It bears the characteristic distal paired roller-joint articulation with the first phalanx of digit IV. The exposed semicircular articulation is smaller than the largely buried one below it, traces of which are visible. This suggests that the specimen is exposed in ventral aspect, the ventral articulation being the smaller one.

PHALANGES. DORCM G.100 is a phalanx from the 'Middle Purbeck Beds' of Langton Matravers originally belonging to the J. C. Mansell-Pleydell Collection. It was listed by Delair (1958 p.71), but is determinable only as a pterodactyloid phalanx.

BMNH 48387 is the register number for a collection of phalangeal fragments from the S. H. Beckles Collection, all originating from the 'Middle Purbeck' of Durlston Bay. Most are indeterminate, but one represents the proximal region of phalanx 1 of the wing finger – digit IV. It bears the characteristic cup-shaped proximal articulation formed partly by the extensor process.

TIBIA. BMNH R.5798 (Fig. 10B) is a large and very slender tibia collected from the Swanage area by S.L. Wood in 1919, and originally identified as a phalanx. It is 205 mm long and poorly preserved but appears to be a left tibia visible in posterior aspect. It must have belonged to a large, long-legged pterodactyloid, and may well be a ctenochasmatid tibia.

DISCUSSION

Chronological ranges of pterodactyloid families
The recognition of ctenochasmatids and ornithocheirids in the Tithonian-Berriasian of England does not significantly change our perception of the geographical distribution of these forms but does extend their known chronological ranges, and also alters the probable range of the Azhdarchidae.

The Ctenochasmatidae were already known from the Upper Jurassic of Europe. The Purbeck *Plataleorhynchus* and *Gnathosaurus* do not represent an extension to their known geographical distribution but may represent a slight chronological extension up into the earliest Cretaceous.

The Azhdarchidae, previously suggested to extend down to the base of the Cretaceous, on the basis of the cervical vertebra from Purbeck, may not appear until later in the record. The discovery of *Plataleorhynchus* does demonstrat

that ctenochasmatids as large as the Chinese *Huanhepterus* were present in Europe. *Huanhepterus* is remarkable for the extreme elongation of the middle series cervical vertebrae and it is probable, though not demonstrable, that the long cervical vertebra from Purbeck belongs to either *Gnathosaurus* or *Plataleorhynchus* and that members of both of these genera had long *Huanhepterus*-like necks. Howse (1986) suggested that the long cervical SMC J5340 from Purbeck represented an early record of an azhdarchid pterodactyloid, and that ctenochasmatids were relatives of the azhdarchids, sharing neck elongation but exhibiting it to a lesser degree. An alternative possibility is that SMC J5340 and BMNH 48387 belonged to a large ctenochasmatid and that the ctenochasmatids had entirely similar cervical series to the azhdarchids which may or may not have been present at the Jurassic-Cretaceous boundary.

The Ornithocheiridae have been described from several localities in the Cretaceous of England, the previous earliest record being *O. sagittirostris* from the Valanginian Hastings Sand of St Leonards on Sea, Sussex. The occurrence of an ornithocheirid in Tithonian-Berriasian strata is a significantly earlier record, and shows that the group was present in the uppermost Jurassic. This implies that ornithocheirids were present at the time that the Solnhofen Limestone was being deposited, and the possibility that one or more of the many Solnhofen pterodactyloids may be primitive or juvenile ornithocheirids should be explored.

Cladograms of possible pterodactyloid relationships published by Howse (1986 fig.11) and Bennett (1989 fig.3) share the conclusion that most of the higher pterodactyloids can be grouped in two major clades – the 'long-spined' forms with tall cervical neural spines (Ornithocheiridae and Pteranodontidae), and 'long-necked' forms (some Pterodactylidae, Ctenochasmatidae, Pterodaustridae and Azhdarchidae). Long-necked forms have been known from the Tithonian Solnhofen Limestone since *Pterodactylus antiquus* was first described in 1812, but the new Purbeck material confirms that the presumed 'long-spined' sister-group was also present at the Tithonian-Berriasian boundary. If Bennett's cladogram is accepted, this would also imply that those pterodactyloid families which branched off further down the cladogram – the Nyctosauridae and the Dsungaripteridae – were also present in the late Jurassic, though they are known only from Cretaceous specimens at present. The relationships of pterodactyloids are not yet so robustly established that we can draw firm conclusions about their phylogeny. However, it increasingly appears that the major family-level groups of pterodactyloids had diversified by the beginning of the Cretaceous although most are not represented until at least the Valanginian.

The Purbeck vertebrate fauna

The Purbeck Limestone Formation produced one of the first diverse assemblages of mid-Mesozoic continental vertebrates to be collected in the mid-19th century, principally from the Beckles Pit and Durlston Bay, and largely comprised of lizards, crocodiles, turtles, mammals and a few dinosaurs. For much of this century, little new material was collected and the known tetrapod fauna of the Purbeck Limestone Formation has remained relatively unaltered, subject to inevitable taxonomic revisions from time to time. However, recent systematic collecting of microvertebrate material from quarries around Langton Matravers by P.C. Ensom, and a series of fortuitous discoveries in the field and in museums, is adding numerous new forms to this Tithonian-Berriasian continental fauna.

The new microvertebrate assemblages collected by Ensom have proved to contain four species of lissamphibian comprising a frog, two types of salamander (one a batrachosauroidid), and an albanerpetontid (Ensom, Evans & Milner 1991), together with three new genera of multituberculate mammal (Kielan-Jaworowska & Ensom 1992; 1994). A fortuitous discovery in Durlston Bay has added the large sphenodontid *Opisthias* to the Purbeck fauna (Evans & Fraser 1994), and reassessment of older material has added the sphenodontid *Homoeosaurus* (Whiteside 1986), a new anguimorph lizard (Evans, 1994) and the pterodactyloids described in this work.

As a result of these and potential further additions, the Purbeck fauna is becoming one of the richest mid-Mesozoic continental tetrapod assemblages known, comparable to those of the Late Cretaceous of North America and Mongolia. Given that the assemblage has been collected from a restricted range of strata over a few square miles, it is likely to represent a genuine fauna of coexisting vertebrates and consequently has considerable potential for palaeoecological studies. It has always been clear that there was a substantial freshwater component to the Purbeck fauna, as evidenced by the presence of a diversity of turtles and crocodiles. The discovery of a range of lissamphibians, together with two pterodactyls specialised for feeding on small aquatic organisms, further emphasises the freshwater-marginal source of much of the fauna.
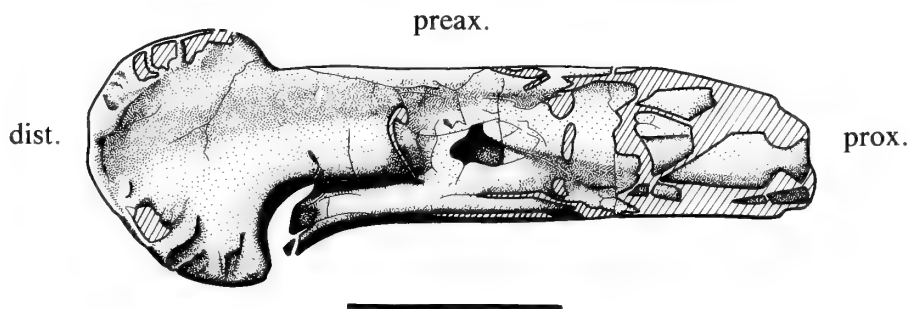
ig. 11 Pterodactyloidea *incertae sedis*. BMNH 48380 fourth metacarpal in ventral aspect. Abbreviations as for figure 9. Scale = 10 mm.

for his meticulous preparation of the new specimens. Our work on this material benefited greatly from discussions with Dr Wellnhofer and the typescript also benefited from comments from Mr Paul C. Ensom (York Museum). The photographs were provided by the Photographic Unit of the Natural History Museum, London. This work was funded by the Natural Environment Research Council under Grant GR3/8053.

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Palaeontology of the Qahlah and Simsima Formations (Cretaceous, Late Campanian-Maastrichtian) of the United Arab Emirates-Oman Border Region

CONTENTS

Preface

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The eight papers in this volume describe the Upper Cretaceous macrofossils collected by members of the Palaeontology Department of The Natural History Museum and others during their investigations of the Qahlah and Simsima Formations in the United Arab Emirates-Oman mountain area. The photograph above shows the spectacular unconformity at an exposure 1 km south of Jebel As-Safir in the Jebel Huwayyah area, between the sub-vertical Jurassic cherts of the Haliw Formation, and the overlying near-horizontal carbonate sequence of the late Upper Cretaceous Simsima Formation. The Haliw Formation is part of the Hawasina Group that contains mantle-derived ophiolites elsewhere, and is an obducted nappe complex that was thrust into position during the mid-Upper Cretaceous and forms the basement beds below the unconformity. The rudist-rich Upper Campanian/ Lower Maastrichtian Qahlah Formation is absent at this locality, being overlapped by the Simsima Formation which lies directly on the truncated beds of the basement. The Simsima Formation yielded most of the other macro-fossils, including 45 species of echinoids belonging to 33 genera, which is one of the most diverse assemblages of echinoids in the Upper Cretaceous known anywhere in the world. The field collecting and work were made possible by a continuing grant to Peter J Whybrow, The Natural History Museum, from the Abu Dhabi Company for Onshore Oil Operations, and in particular we would like to thank Dr Terry Adams, Mr David Woodward and Mr Kevin Dunne, successive General Managers of ADCO for their support and encouragement. In addition we thank Mr Nabil Zakhour, Head of Public Affairs and Dr Jose E de Matos, Senior Geologist, ADCO, for their sustained assistance. The ADCO grant for research in and around the Emirate of Abu Dhabi forms part of the Natural History Museum's *'Global Change and the Biosphere'* research theme.

Late Cretaceous carbonate platform faunas of the United Arab Emirates-Oman border region

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CONTENTS

SYNOPSIS. The stratigraphy and macrofauna of the Qahlah and Simsima Formations is described for 14 sections along the western margins of the North Oman Mountains between Al Ain and Al Dhaid. These are the earliest autochthonous deposits following emplacement of the Semail ophiolite complex and are dated, on the basis of ammonites, inoceramid bivalves and echinoids, as latest Campanian to Maastrichtian in age. Deposition over a deeply weathered surface of ultrabasic rocks commenced with nearshore conglomerates, grits and cross-bedded sands which, in places, have an *in situ* bivalve fauna. Clastic input was abruptly terminated by a sea-level rise and replaced by carbonate deposition in the early Upper Maastrichtian. The basal carbonate bed is composed of coarse shoreface reefal debris formed during rapid transgression. This is overlain by a highly fossiliferous series of muddy carbonate sands deposited in shallow water around wave-base. There is indirect evidence for algal stands from the associated macrofauna, and level-bottom thickets of corals/rudists are present. Upper beds are well-washed carbonate sands rich in larger benthic foraminifers but with few macrofossils that were deposited in broad subtidal flats. In places these are overlain by deeper shelf-basinal marls. Bed by bed faunal lists for each section are provided.

INTRODUCTION

The Oman Mountains form a prominent arcuate range along the northeastern corner of the Arabian Peninsula. Their geological history is complex, but work by Glennie *et al.* (1974), Glennie (1977), Hughes-Clarke (1988) and contributers to Robertson *et al.* (1990) has done much to improve our understanding of this region. The rocks forming the Oman Mountains can be divided into seven major geological units, ranging in age from late Proterozoic to early Tertiary. Of direct interest here are the Hawasina Group, the Semail Nappe and the Maastrichtian to early Tertiary autochthonous marine clastics and carbonates. The Hawasina Group is formed of tectonic slices of Permian to mid-Cretaceous sedimentary sequences deposited over the ocean floor and continental slope of the Arabian continent. They were obducted onto the continental margin of the Arabian platform during the Upper Cretaceous. The Semail Nappe represents a massive slice of former oceanic crust, generated by subduction-related spreading during the Cenomanian-Turonian and emplaced before the Upper Campanian. Both are overlain by marine sediments of Maastrichtian to Palaeocene age. Initially these beds were deposited around the newly emergent margins of the Arabian shield, following the obduction event. Later, a broad carbonate platform formed over the region as it subsided. Only remnants of this once widespread succession now remain, forming small jebels along the western margins of the Oman Mountains.

The late Cretaceous to early Palaeocene rocks are conventionally divided into three units (Skelton *et al.* 1990), which are, from bottom to top:

1. The **Qahlah Formation** – a marine clastic sequence of sands and conglomerates of late Campanian or early Maastrichtian age.
2. The **Simsima Formation** – a platform carbonate sequence of Maastrichtian age.
3. The **Pabdeh Group** – a basal limestone conglomerate of reworked Simsima Formation with an erosive base, of

presumed early Palaeocene age, overlain by thin-bedded basinal marls of late Palaeocene age.

Until recently little was known of the fauna of the late Cretaceous rocks of this region. The first published account of Cretaceous fossils was that of Carter (1852), who described late Cretaceous sediments of the Hadramaut region of southeast Oman. Parts of the fauna collected by Carter were described by Duncan (1865) and are Cenomanian in age. Lees (1928) gave the first authoritative account of the geology of the Oman Mountains and provided much new palaeontological data. He described late Cretaceous faunas from several localities, including Jebel Bu Milh ('Jabal al Milah in Wadi Sharm'), where he recorded and described 39 taxa of gastropods ('the product of an hour's collecting'). Clegg (1933) also described a small number of late Cretaceous species from Oman, but without stratigraphic details.

In the past few years there has been renewed interest in the geology and palaeontology of the late Cretaceous deposits around the fringes of the Oman Mountains. The regional setting of these deposits was outlined by Alsharham & Nairn (1990, 1994), who also described lithofacies and listed microfauna for type sections. The late Cretaceous stratigraphy and faunas from the south western Oman Mountains (Dhofar region, Oman) were studied by Platel & Roger (1989), Roger et al. (1989) and Roman et al. (1989). Late Cretaceous ammonites, echinoids, foraminifera and calcareous algae were described from the central Oman Mountains (Smith et al. 1990, Kennedy & Simmons 1991). To the north, along the United Arab Emirates-Oman border region, Skelton et al.

(1990) studied key late Cretaceous sections from both a sedimentological and palaeontological standpoint. They published lithostratigraphic sections and faunal lists for these sections, with particular emphasis on the rudist bivalve faunas, from which they were able to provide the first detailed assessment of late Cretaceous palaeoenvironments for the region, demonstrating that the carbonate succession recorded a variety of facies ranging from intertidal to shelf basinal settings. Finally, there are a series of papers documenting part of the diverse echinoid fauna (Ali 1989, 1992a,b) and a few of the molluscs and corals from this region (Ghalib, 1989, 1990; Metwally 1992).

Our interest in the faunas of this region began in 1984, when Dr. S. Nolan (then at the University of Swansea) and Dr. P.W. Skelton (Open University) brought back their collection of late Cretaceous fossils for identification. This, together with material brought to the Natural History Museum for identification by amateur collectors (notably, Mrs Valerie Chalmers), alerted us to the importance of the Maastrichtian faunas of the western fringes of the Oman Mountains. In April, 1991, A.B. Smith carried out a preliminary survey of some late Cretaceous fossil localities along the Oman-United Arab Emirates border. The echinoid fauna proved to be exceedingly rich and also remarkably well-preserved, and without doubt represents the most important Maastrichtian Tethyan echinoid fauna yet known.

During this initial survey it became rapidly apparent that the molluscan and coral faunas were also exceedingly rich and likely to be of equal importance, both in terms of new taxa and their significance for understanding late Cretaceous
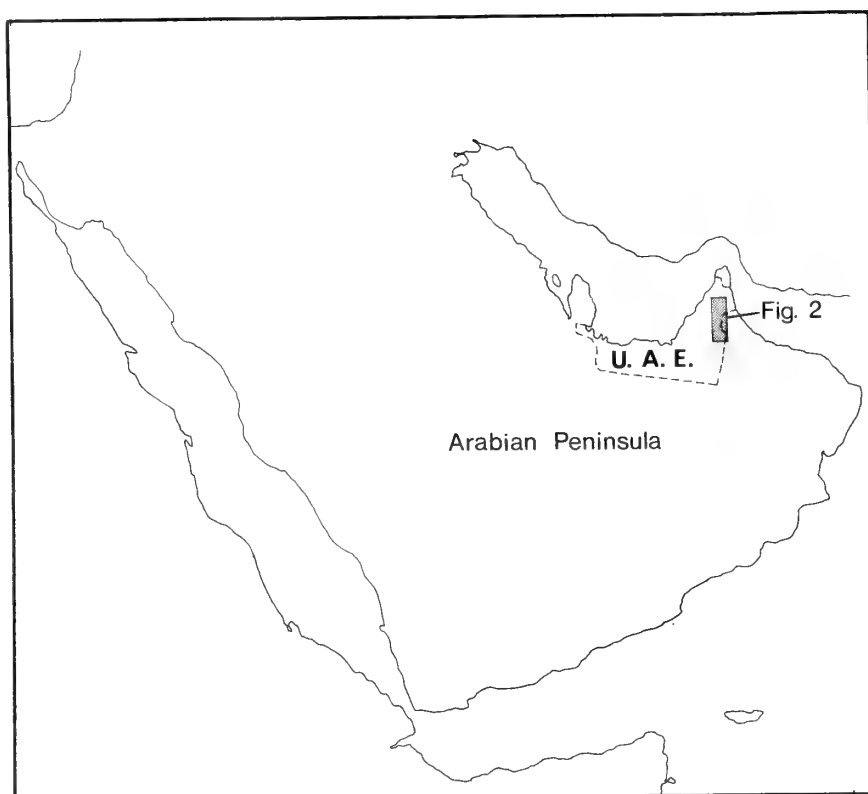
Fig. 1 Map of the Arabian Peninsula showing the area of study.

benthic community structure. Indeed, the small collections brought back to London for examination here by relevant experts generated considerable interest. Consequently a second expedition was mounted to study the entire macrofauna from these important sections and to investigate the lithofacies and palaeoenvironments in more detail. In January, 1992 three of us (ABS, NJM, ASG) spent two weeks exploring, logging and collecting from the late Cretaceous outcrops that form the western margins of the Oman Mountains along the United Arab Emirates Oman borders region. It is the results of these two bouts of fieldwork that form the subject of the following papers.

STUDY AREA

Our study area lies along the border between the United Arab Emirates and the Sultanate of Oman (Fig. 1). Outcrops in this region comprise small, generally outlying jebels along the western fringes of the Oman Mountains. Collection and logging was carried out at eight sites ranging from Jebel Huwayyah in the south to Jebel Faiyah in the north (Fig. 2). Sections were measured at each jebel and macrofauna collected or noted bed by bed. Details of the outcrops studied are as follows:

1. Jebel Huwayyah (Figs 2, 3). Two sections were logged and their faunas collected systematically.
Jebel Huwayyah, section 1. Southeastern corner of the U-shaped Jebel immediately to the north of the dirt track and about 3 km SE of the northwestern corner of the jebel, 10 km NE of Al Ain, United Arab Emirates. Map reference: Buraymi Sheet 1:100,000 NG–40–140; grid reference 842,878.
Jebel Huwayyah, section 2. Western face of the eastern limb of the jebel approximately 2 km SSE of the northwestern corner of the jebel, 10 km NE of Al Ain, United Arab Emirates. Map Reference: Buraymi Sheet 1:100,000, NG–40–140; grid reference 823,877.

2. Jebel Bu Milh (Fig. 3). Two sections were studied in detail.
Jebel Bu Milh, section 1. Western face of a prominent ridge at the northwestern tip of the jebel, 10 km NW of the village of Mabdah, Oman. Map reference: Buraymi Sheet 1:100,000 NG–40–140; grid reference 895,075.
Jebel Bu Milh, section 2. Southeastern corner of a prominent knoll, isolated from the main jebel at its northern end, some 10 km NW of Mabdah, Oman. Map Reference: Buraymi Sheet 1:100,000 NG–40–140; grid reference 906,075.

3. Jebel Rawdah (Figs 2, 4B). Six sections were examined in detail and a further two briefly investigated but not logged or systematically sampled. Logged sections are as follows:
Jebel Rawdah, section 1. Slope and cliff at the eastern end of the northern flank of a valley some 50 m east of the head of the valley, 3 km east of quarry weigh-bridge and site office, Jebel Rawdah, east of Al Madam, United Arab Emirates. Sumayni sheet NG–40–14A 1:100,000; grid ref. 925,528.
Jebel Rawdah, section 2. Slope and cliff on northern side of Jebel Rawdah, about 2 km east of quarry weigh-bridge and site office, Jebel Rawdah, east of Al Madam, United Arab Emirates. Sumayni sheet NG–40–14A 1:100,000; grid ref.
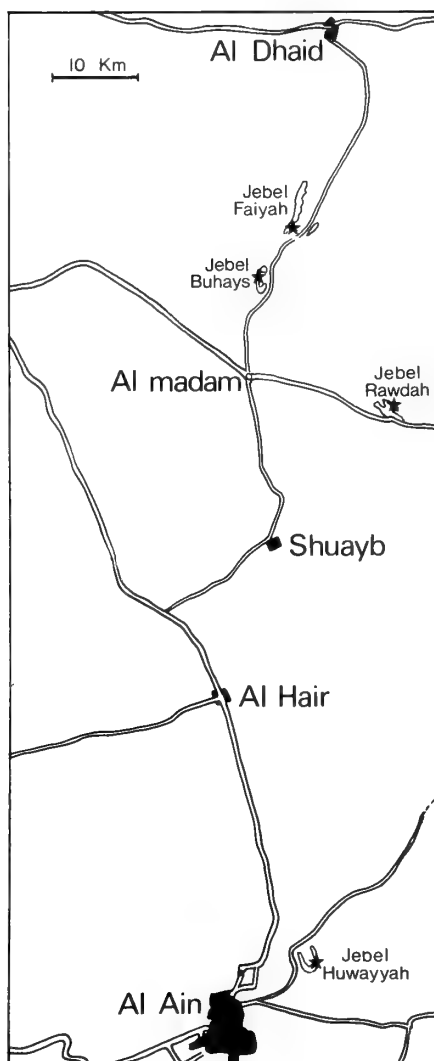
Fig. 2 Locality map showing the position of the four major jebels studied (asterisked) where there are important outcrops of late Cretaceous sediments. For regional placement see Fig. 1.

913,544.
Jebel Rawdah, section 3. Slope and cliff on south side of valley from 200 to 600 m east of the head of the valley, about 3 km east of quarry weigh-bridge and site office, Jebel Rawdah, east of Al Madam, United Arab Emirates. There were three measured sections, labelled from west to east a, b, and c. Sumayni sheet NG–40–14A 1:100,000; grid refs 932,528 (section 3a): 928,527 (section 3b) and 927,527 (section 3c).
Jebel Rawdah, section 4. Slope and cliff at the eastern end of the northern flank of a valley, 600 m east of the head of that valley, 2.5 km east of quarry weigh-bridge and site office, Jebel Rawdah, east of Al Madam, United Arab Emirates. Sumayni sheet NG–40–14A 1:100,000; grid ref. 928,531.

4. Jebel Buhays (Figs 2, 4A). Two sections were logged and their faunas systematically collected. A third section (2), exposing the lowest beds of the sequence was impossible to
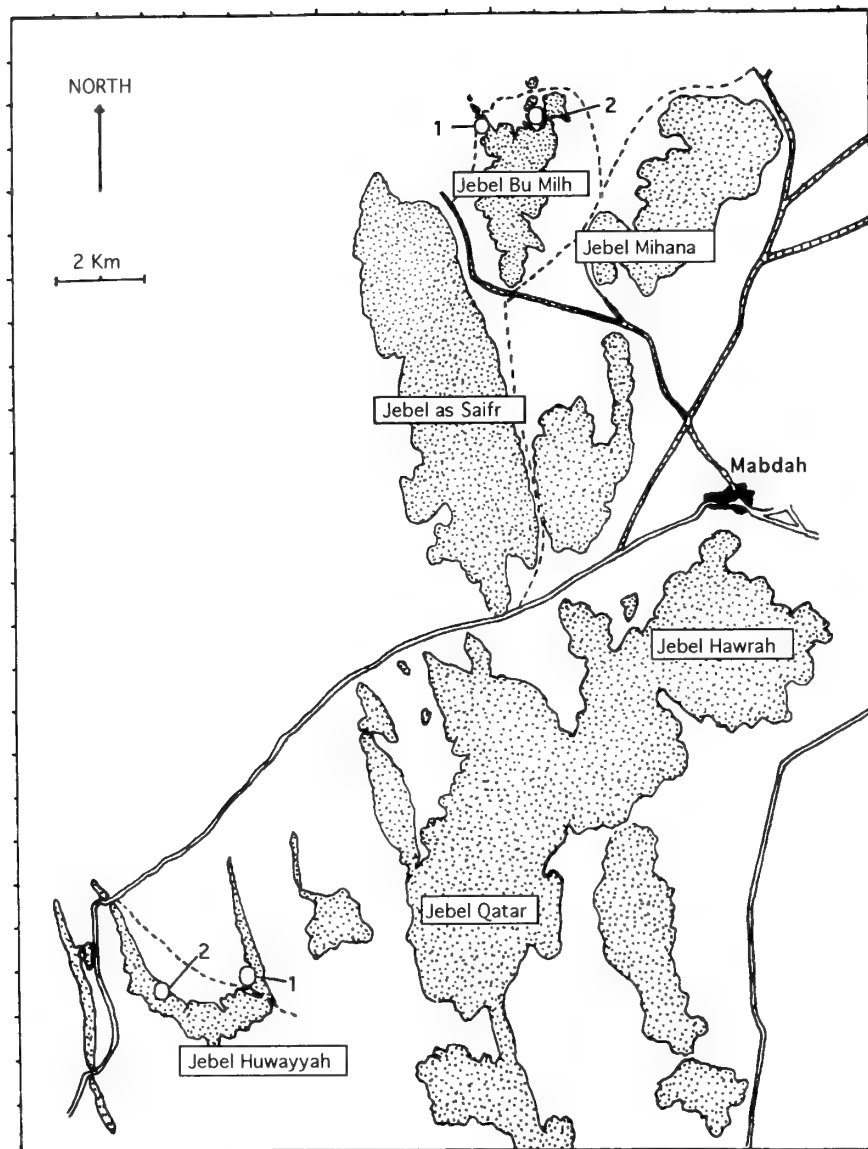
Fig. 3   Detailed locality map for Jebel Huwayyah and Jebel Bu Milh. 1, 2 = studied sections. For regional placement see Fig. 2.

log, but collections were made from the scree slope.

Jebel Buhays, section 1. East face of the most northerly hill forming Jebel Buhays, 4 km north of Al Madam, United Arab Emirates. Dhayd Sheet 1:100,000, NG–40–107; 780,681. A second section 300 m to the south and forming another small hill was also examined and collected from, but no detailed section was made.

Jebel Buhays, section 2. Scree slope at the southwestern corner of Jebel Buhays, 4 km north of Al Madam, United Arab Emirates. Dhayd Sheet 1:100,000, NG–40–107; grid ref. 779,668. No measured section could be made, but the beds are almost vertical here and the scree material is all derived from the lowest few metres of the sequence.

Jebel Buhays, section 3. Northeastern corner of Jebel Buhays, just southeast of a television mast, 4 km north of Al Madam, United Arab Emirates. Dhayd Sheet 1:100,000, NG–40–107; grid ref. 788,670.

5. Jebel Thanais (Fig. 4A). Northeastern side of the jebel, about 4 km north of Al Madam, United Arab Emirates. Dhayd Sheet 1:100,000, NG–40–107; grid ref. 783,699.

6. Jebel Aqabah (Fig. 4A). Southwestern face of jebel, forming a steep cliff about 200 m northeast of the tip of Jebel Thanais and about 4 km north of Al Madam, United Arab Emirates. Dhayd Sheet 1:100,000, NG–40–107; grid ref. 785,698.

7. Jebel Faiyah (Figs 2, 4A). One section was logged in detail. A further three were explored but found to be unprofitable: collections were made from only one.

Jebel Faiyah, section 1. Eastern scarp face from the southern nose of the jebel northwards for 500 m, 5.5 km north of Al Madam, United Arab Emirates. Detailed logs were made at the northern end of the section (section 1a) and approxi-

mately midway along (section 1b). Dhayd Sheet 1:100,000, NG–40–107; grid ref. 800,697 to 802,702.

Jebel Faiyah, section 2. Eastern scarp face of the jebel approximately 3 km NNE of the southern tip of the jebel, and 8 km N of Al Madam, United Arab Emirates. Dhayd Sheet 1:100,000, NG–40–107; grid. ref. 806,722. All but the lowest 2 metres of outcrop was highly indurated and thus fossils collected come from only these basal beds.

8. Qarn Murrah (Fig. 4A). Northeastern slope of the qarn, some 8 km west of the northern tip of Jebel Faiyah and 15 km north of Al Madam, United Arab Emirates. Dhayd Sheet 1:100,000, NG–40–107; grid ref. (approx.) 760,795. The section here was small and the rocks hard and well-lithified, making collecting difficult. No section was logged.

LITHOFACIES AND FAUNAL ASSEMBLAGES

A total of 14 sections were logged and their macrofauna recorded. Lithological samples were collected systematically from the thickest sequence, (Jebel Rawdah, section 2), and sectioned for petrographic analysis. The lithological descriptions given for other sections are based solely on field observations and are consequently of a preliminary nature. The results of this work are summarized in the measured sections (Figs 5–11) and in the faunal lists of the Appendix. As the successions in the various jebels differ significantly and correlation between jebels was not initially obvious, each succession is documented in turn before attempting a synthesis.

Jebel Rawdah (Figs 5–7)

1. Sedimentary lithofacies at section 2. From field logging and petrographic analysis we recognize the following major lithofacies:

Facies 1. The succession commences with an ultrabasic clast conglomerate (bed 1). This can reach more than 10 m in thickness in places, and comprises well-rounded clasts of mean size 10–20 cm. There are rare rounded fragments of rudist and occasional acteonellid gastropod shells. Similar sediments in the region have been interpreted as beach deposits by Skelton *et al.* (1990), a view supported in our interpretation.

Facies 2. There then follows a mixed clastic-bioclastic coarse sand, with relatively well-rounded coarse sand to gravel-sized clasts, ca. 1 m thick (beds 2–4). This includes up to 20% ultrabasic sand. The high sphericity and excellent sorting of the clasts indicates these sediments accumulated in a very high-energy environment; either intertidal or very shallow subtidal. We interpret these as shoreface sands.

Facies 3/4. The majority of lower beds in the succession are poorly sorted mollusc-coral-foraminiferal packstones that contain components of three size classes: (i) clay and silt-grade carbonate, now replaced by a weak ferroan calcite microsparite cement; (ii) well-rounded, fine sand-grade particles, with a sizeable component of ultrabasic grains in the lower beds, as well as rolled and bored mollusc and echinoderm debris; (iii) diverse larger bioclasts which vary in composition from bed to bed. There are two broad facies distinguishable in hand specimen on the basis of the major clast component.

Facies 3 is a poorly sorted calcarenite rich in mollusc clasts (especially rudist clasts) as well as obvious ultramafic sand-
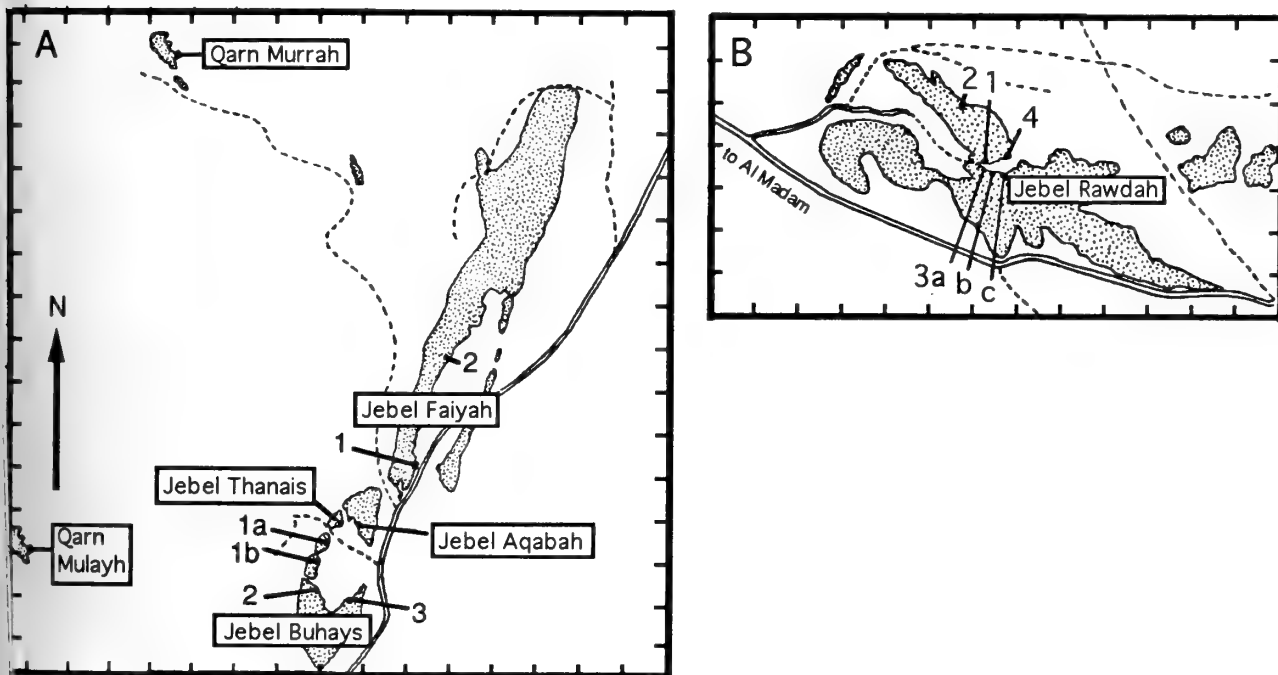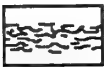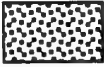
Fig. 4 Detailed locality map for Qarn Murrah and Jebels Buhays, Thanais, Aqabah and Faiyah (map A), and Jebel Rawdah (map B). 1, 2, 3, 4 = studied sections. For regional placement see Fig. 2.

Figures 5 - 11. Measured sections through the late Cretaceous Qalah and Simsima Formations. Locality details for each named section are given in Figures 2 - 4 and in the text. Logs are drawn to a scale of 5 mm = 1 m for Figs 5, 6, 9 - 11 and 4 mm = 1 m for Figs 7 and 8. Lithological data are based on field observations except for Jebel Rawdah, section 2. Faunal assemblages noted in the right-hand column are also largely based on field observations; full faunal lists for each section are given in Appendix 1.

Symbols used are as follows:-

Bioturbation

Siliciclastic sands & conglomerates

Coarse, poorly sorted bioclastic wackestones

Poorly-sorted bioclastic packstones with major orbitoid foraminifer content

Well-sorted bioclastic packstones

Red-weathering marly seams and wackestones

Weathered serpentenite (Semail complex)

Rudists (*Dictyoptychus*)

Rudists (*Hippurites*)

Rudists (large *Vaccinites*)

Infaunal bivalves (*Scabrotrigonia*)

Bivalves (undifferentiated)

Gastropods (*Campanile*)

Gastropods (*Acteonella*)

Gastropods (undifferentiated)

Corals

Stromatoporoids

Echinoids

Algal nodules

Loftusia (benthic foraminiferan)

grade clasts. This makes up the lower beds (beds 5–10) and includes various thin coquina lenses and horizons of coarse coral and rudist debris.

Facies 4 is characterized by an abundance of orbitoid foraminiferan clasts, with fragments of the rudist *Dictyoptychus* common in lower beds (beds 11–12) and of corals in upper beds (beds 15–19). Furthermore, in these higher beds there are also layered blebs of mud-grade carbonate, incorporating sand-grade bioclasts, which are storm-reworked pellets of mud-grade sediment.

Skelton *et al.* (1990) interpreted facies 3 and 4 as deposits formed in a point bar and tidal channel system. However, the original presence of significant quantities of mud-grade carbonate (probably algal aragonite) in this facies, together with its overall poor sorting is taken as evidence of deposition below normal wave-base. The sand-grade component, which

is well-rounded and was originally well-sorted, was probably washed in from shallower water (intertidal to shallow subtidal) by storm activity.

Metre- to several metre-scale bedding cycles (most obviously expressed in banded rhodolite development) are apparent in this facies. The origin of such cyclicity is enigmatic, but the deeper-water setting proposed above militates against their being tidal channel in origin.

Facies 5. The upper part of the succession (comprising beds 19–28) is composed of well-sorted, well-rounded sand-grade bioclasts, grain supported and originally containing little or no calcite mud. There are rare larger (up to 1 cm) bioclasts. The foraminiferal component is dominant (50–60%) and includes both broken and rolled orbitoids, entire small rotalines and miliolines. Up to 10% dasycladacean algae also occurs. This facies was deposited significantly above wave-

Jebel Rawdah 2 (lower part)

Unit	Lithology	Fauna
23	Massive well-sorted packstones with scattered orbitoids	Campanile
22	Prominent parting	Occasional Hemipneustes
	Massive well-sorted packstones with scattered orbitoids	
21	Nodular well-sorted bioclastic sand	Echinoid level - Hemipneustes, Pygurostoma, Petalobrissus, Noetlingaster; Barbatia, Pycnodonte, Campanile and gastropod moulds
	Red marly parting	
20	Nodular well-sorted bioclastic sand	Pygurostoma, Noetlingaster, Hemipneustes
19	Bioturbated orbitoid-rich bioclastic packstone	Petalobrissus, occasional Globator, Faujasia; Large Astrogyra; Dictyoptychus, Tylostoma and other molluscs
18	Orbitoid-rich wackestone	Abundant Cunnolites and gastropods
17		Loftusia common
16		Bournonia
15	Poorly sorted bioclastic wackestones rich in orbitoids and with rhodolite bands	Petalobrissus, occasional Hemipneustes; Loftusia in levels; gastropods common; Cunnolites moderately common
14	Red-weathering, flaggy bedded silty calcarenite	Hardouinia, Hemipneustes, Petalobrissus
13	Poorly sorted orbitoline-rich bioclastic wackestone	Alternating Dictyoptychus and Cunnolites beds, with Loftusia and Petalobrissus; Giant Dictyoptychus
12		Cucullaea, Pholadomya; Petalobrissus, Globator
	Nodular, coarse bioclastic wackestone with orbitoids	Noetlingaster, Zuffardia, Petalobrissus; Cunnilites; Modiolus
11		Abundant Petalobrissus; occasional mollusc debris
	Orange parting	Echinoid-rich level with Porosoma Bournonia abundant
10		Lots of broken molluscan debris, rare Dictyoptychus and stromatoporoids; rare Faujasia, Goniopygus and Orthocyphus
9	Grey poorly-sorted bioclastic packstone with siliciclastic grains	Molluscs, Faujasia, rare Goniopygus, Orthocyphus
		Echinoid-rich level
6-8		Molluscan debris
5		Echinoid-rich level
		Rolled and bored stromatoporoid heads, ocassional compound corals and Dictyoptychus
4	Sandy calcarenite	Molluscan debris; abundant Bournonia; Faujasia, Goniopygus, Porosoma, Salenia
3	Boulder conglomerate	
2	Sandy calcarenite	Rudist and other molluscan debris; Faujasia
1	Boulder conglomerate	

Jebel Rawdah 2 (upper part)

Unit	Lithology	Fauna
28		Large Dictyoptychus and other poorly preserved rudists abundant
27	Massive-bedded well-sorted packstone with scattered orbitoids and other bioclastic debris	Occasional levels of echinoid and mollusc debris seen in cross-section
26	Nodular, red-weathering silty calcarenite	Petalobrissus, Hemipneustes, Noetlingaster, Pygurostoma, Faujasia; Campanile
25		
24		Noetlingaster
23	Massive well-sorted packstones with scattered orbitoids	Campanile

Fig. 5   Measured section made at Jebel Rawdah, section 2 (see Fig. 4B for locality).

base in a high energy environment, as indicated by the high degree of sorting and lack of mud-grade carbonate.

2. Succession and faunal assemblages (Figs 5–7). Lateral variation is considerably greater here than at any other jebel. Of particular note is the marked attenuation of the entire lower part of the succession eastwards along Jebel Rawdah 3 (Fig. 7). However, although there is marked variation in bed development from one section to the next, the same general succession can be identified at them all.

The basal pebble to boulder conglomerate varies tremendously in thickness, being best developed at Jebel Rawdah 3a and thinnest at Jebel Rawdah 4. There is very little in the way of sand and grit lenses developed, the entire sequence being exceedingly coarse. However, rare *Acteonella* are present in the upper part of the sequence at Jebel Rawdah 3.

The coarse siliciclastics are succeeded by a thin transitional sandy calcarenite facies quickly followed by grey, shelly bioclastic limestones with obvious scattered sand-sized grains of ophiolite. These basal calcarenites are relatively coarse and are well-lithified. At several horizons the beds contain rolled and often bored heads of the compound coral *Actinacis*, some up to 30 cm in diameter, as well as a variety of allochthonous compound corals and mollusc debris. The infaunal cassiduloid *Faujasia eccentripora* is the only obvious autochthonous element in these beds. The basal bed at Jebel Rawdah 4 is notable for the abundance of transported hippuritid and *Durania* rudists. Within the succession at section 2 there are two closely-spaced shell-rich partings with many echinoids, notably *Goniopygus*, *Phymotaxis* and *Orthocyphus*.

Towards the top of this calcarenitic succession is a prominent, orange-weathering, silt-enriched parting (top of bed 10, section 2). This bed is thickest at Jebel Rawdah 2 and has the same echinoid fauna as found below. The overlying beds are still bioclastic calcareous sands but are more poorly sorted, and in places include significant amounts of sand-grade siliciclastics (e.g. section 1, bed 1). They contain the solitary discoidal coral *Cunnolites* and the infaunal bivalves *Cucullaea*, *Pholadomya* and, in places, *Scabrotrigonia*. Orbitoid Foraminifera occur but only in minor abundance.

Overlying these poorly sorted bioclastic limestones come orbitoid-rich packstones, with abundant specimens of the infaunal cassiduloid echinoid *Petalobrissus*. At the base there is a distinctive infaunal echinoid assemblage dominated by the cassiduloid *Zuffardia* and the epifaunal regular echinoid *Noetlingaster*. One to three metres above the base of orbitoid-rich limestones there is a prominent horizon of very large examples of the rudist *Dictyoptychus*, probably in life position. The succeeding 2–3 metres at Jebel Rawdah 2 consist of beds with *Dictyoptychus* alternating with beds rich in the solitary discoidal coral *Cunnolites*, the larger benthic foraminifer *Loftusia*, and the infaunal cassiduloid echinoid *Petalobrissus*. It is at about this level that the ammonite *Brahmaites (Anabrahmaites) vishnu* (Forbes, 1846) was found at Jebel Rawdah 1. A second major silt-enriched level occurs above this, and these flaggy beds yield a fauna of large infaunal cassiduloid and holasteroid echinoids (*Hardouinia*, *Hemipneustes*).

There then follows a succession of rather fine, muddy, thoroughly bioturbated, bioclastic limestones with orbitoid Foraminifera and bands of rhodolite nodules. There are occasional infaunal holasteroid echinoids (*Hemipneustes*), but the predominant component of the fauna are the solitary

discoidal corals (*Cunnolites* and *Asteraea*) and a variety of gastropods, together with the larger benthic foraminifer *Loftusia*.

The succeeding bed (bed 19, section 2) contains large compound corals (*Astrogyra*) and rudist material. This bioclastic limestone also has occasional large infaunal echinoids and a mixture of other molluscs.

The next few metres are composed of well-sorted, red-weathering, silt-rich calcarenites. They have a significant fine siliciclastic content, particularly in the *Hemipneustes* beds (bed 21, section 2).

There then follows a thick and fairly monotonous sequence of well-sorted calcarenites with sparse to moderate numbers of orbitoid Foraminifera. This facies has little in the way of macrobenthos, other than the occasional *Dictyoptychus*, *Noetlingaster* or *Campanile*. There is, however, one distinct nodular, red-weathering, silt-enriched calcarenite level which has a diverse fauna of infaunal cassiduloid and holasteroid echinoids towards the top.

Large, poorly preserved rudists occur in abundance at the top of the sequence and the succession is terminated by an unconformity.

3. Palaeoenvironmental interpretation. It is clear that at Jebel Rawdah local sedimentation patterns were controlled by topographic variation of the underlying sea-floor. In particular, the south-eastern corner appears to have been relatively starved of sediment compared, for example, to the northern flank of the jebel.

In environmental terms deposition commenced with pebble conglomerates laid down in a near-shore high-energy environment around the newly emergent obduction complex. These were replaced rapidly, as the obduction complex subsided and the region became flooded, by coarse, poorly sorted carbonate sands. These contain significant amounts of reefal debris and represent immediately offshore sands accumulating below wave-base. The following sequence of mixed orbitoid-rich platform shoals alternating with more protected platform bioclastic sands with their gastropod and solitary coral fauna probably represent local variation between topological highs and dips over a broad carbonate platform in probably no more than 10–20 m water depth. Towards the top of the section a regressive phase is marked by a brief period of patch-reef development and the influx of fine siliciclastics. The remainder of the succession is composed of shallow-water calcarenites formed within active wave-base and supporting only a sparse fauna.

Jebel Huwayyah.

1. Lithological succession and faunal assemblage (Fig. 8). The general succession is similar throughout the jebel, though with some lateral variation in bed thicknesses. The lowest beds, best seen at section 1, consist of poorly sorted silts and sands with rare lenses of the oyster *Acutostrea*. The succession passes up into pebble- and grit-sized conglomerates and cross-bedded siliciclastic sandstones, the pebbles being predominantly igneous in origin and well-rounded. Bed 7 is of particular interest because it contains broken fragments of thick-shelled rudists, and occasional pebbles that are encrusted by *Acutostrea* or, more rarely, by small compound corals.

After a small gap in exposure there follows a succession of highly bioturbated, poorly sorted, brown-weathering, silt-rich

Fig. 6 Measured sections made at Jebel Rawdah, sections 1 and 4 (see Fig. 4B for locality).

Fig. 7   Measured sections made at Jebel Rawdah, section 3 (see Fig. 4B for locality).

Jebel Huwayyah 1

Unit	Description	Fauna/Features
19		Agerostrea and Pycnodonte
18	Fine-grained carbonate sands/silts with chert nodules and scattered orbitoids	Proraster
		Thalassinoides burrow systems
17		Agerostrea and Pycnodonte; occasional solitary corals
		Campanile
		Oyster debris
16	More massive, orbitoid-rich, packstone	
15	Bioturbated poorly-sorted bioclastic packstone with orbitoids	Diverse fauna, including abundant gastropods including Campanile; Globator Pygurostoma, Orthopsis; corals, bivalves
14	Coarse, poorly sorted bioclastic packstone	
13	Pebble conglomerate	
12	Silty bioclastic wackestone with calcareous nodules	Scattered Loftusia
11	Bioclastic packstone	Abundant Loftusia; Faujasia; Vaccinites, Spondylus solitary discoidal corals; rare compound corals, ammonites
10	Silty bioclastic wackestone	
9	Rubbly bedded sandy bioclastic wackestone	Abundant Loftusia
8	Pebble conglomerate	
	Cross-bedded, coarse sand with strings of grit	
7	Pebble conglomerate	Rudist fragments; some pebbles oyster encrusted (Acutostrea); bryozoans
6	Cross-bedded, coarse sand with strings of grit	
5		
4	Poorly sorted conglomerates with cross-bedded sand lenses	
3	Fine carbonate sand with scattered clasts	Sparse Acutostrea
2	Poorly sorted conglomerates with sand lenses	
1	Sand with scattered clasts	Small Acutostrea and Gastrochondrites

Jebel Huwayyah 2

Unit	Description	Fauna/Features
8	Bioclastic packstone	Compound corals; Dictyoptychus and Vaccinites; rare ammonites
7		
5	Rubbly bedded sandy bioclastic wackestone	Abundant Loftusia and discoidal solitary corals; diverse molluscs; Hemiaster
4		
3	Rubbly bedded sandy bioclastic wackestone	Abundant Loftusia and discoidal solitary corals; diverse mollusc fauna
1	Rubbly bedded sandy bioclastic wackestone	Abundant Loftusia and discoidal solitary corals; diverse mollusc fauna; Coptodiscus, Glyphopneustes

Fig. 8 Measured sections made at Jebel Huwayyah, sections 1 and 2 (see Fig. 3 for locality).

bioclastic limestones with significant amounts of dark-green, sand-sized, igneous grains. These beds contain abundant specimens of the benthic foraminifer *Loftusia* as well as scattered molluscan debris and occasional infaunal spatangoid echinoids. The large solitary button coral *Cunnolites* is also abundant. Within this facies are two prominent marker limestones that are thicker and better developed on the western limb of the jebel. They contain a rich fauna of compound corals, the hippuritid rudist *Vaccanites* and the occasional large, tall-spired gastropod *Campanile*. None of the rudists are found in life position and the beds appear to represent allochthonous accumulations. However, the base of the upper of these beds is typically rich in *Spondylus* and *Plicatula* that are clearly not transported, as most are preserved with both valves connected. Ammonites, some quite large, are occasionally found at this level, presumably transported into this environment.

Above the *Loftusia*-rich beds comes a sequence of less fossiliferous silty bioclastic carbonate sands, which are in turn succeeded by a thick pebble conglomerate. This conglomerate is composed of very well-rounded clasts, and represents such an anomalous lithofacies change that it must have formed through exposure and reworking of earlier conglomeratic beds. Above the conglomerate siliciclastics abruptly disappear and are replaced by relatively clean bioclastic limestones of the Simsima Formation. This starts with an initial shell-rich bioclastic limestone, followed by 2 to 3 metres of highly bioturbated and poorly sorted bioclastic limestones with sparse sand-grade siliciclastics. These sediments are very fossiliferous, the fauna dominated by shallow infaunal cassiduloids and holectypoids (*Pygurostoma* and *Globator*), infaunal naticids and other gastropods, including *Campanile*. Occasional pectinid bivalves are also present.

Higher beds pass into less fossiliferous and much more massive and well-sorted, orbitoid-rich carbonate sands and silts. There is at least one level of thallasinoid burrows. Rare *Dictyoptychus* are found here. The orbitoid content of the sediments decreases upwards so that higher beds, which contain the epifaunal bivalves *Agerostrea*, *Pycnodonte* and the infaunal spatangoid *Proraster*, are finer-grained carbonate sands or silts with relatively few orbitoid clasts.

2. Palaeoenvironmental interpretation. The succession commences with unconsolidated subtidal sand and cobble beds deposited around the margins of the newly emergent obduction complex. The sequence shallows upwards into the shoreface facies of bed 7, with increasing cross-bedding and coarser clastic content. The clastic supply then sharply diminishes, presumably marking the final flooding of nearby ophiolite islands, and the initiation of carbonate platform development. The poorly sorted *Loftusia*-rich muddy carbonate sands represent extremely shallow-water, back bar or lagoonal deposits formed in a protected environment below wave-base. Coral-hippuritid thickets were able to develop locally and occasional open-water ammonites were washed in. The thin, well-sorted calcarenitic sands with *Faujasia* may represent protected beach-face sands.

A brief regression caused by local uplift led to the exposure of Qahlah Formation conglomerates, or their source rock, and pebble conglomerates were once more briefly deposited in a high-energy shallow marine environment (bed 13). This was short-lived and carbonate platform conditions returned once again, bringing about the more or less complete elimination of siliciclastic components. This presumably marks a renewed phase of subsidence with transgressive seas once more flooding the region and cutting off siliciclastic input. The initial coarse bioclastic fossiliferous sands (bed 14), we interpret as deposits formed at or immediately below normal wave-base. They are replaced immediately upwards by thick beds of shallower-water orbitoid-rich carbonate sands with little macrobenthos, formed within wave-base. These are succeeded in turn by fine carbonate sands and silts suggestive of shelf-basinal conditions.

Jebel Bu Milh

1. Lithological succession and faunal assemblages (Fig. 9). The succession begins, as in Jebel Huwayyah and elsewhere, with a rather thick series of well-rounded pebble conglomerates, grits and coarse clastic sands, with some small-scale cross-bedding. Although largely unfossiliferous, occasional clumps of the rudist *Durania* can be found, apparently *in situ*. Towards the top is a 1–2 m thick conglomeratic sequence, packed with well-sorted shells of the gastropod *Acteonella*, showing good current alignment of individual layers. Occasional specimens of the rudist *Pseudosabinia* also occur. The succeeding clastic sands are strongly cross-bedded and contain occasional *Acteonella* specimens, as well as large logs bored by lithophagid bivalves.

There is then a sharp reduction in the siliciclastic content of the sediments and the succeeding 1.0–1.5 metres are composed of highly fossiliferous calcarenitic limestones with sparse sand-sized quartz grains. The basal bed is a fine, silty calcarenite that is highly nodular and extensively bioturbated. It contains rare nautiloids and ammonites and a rich gastropod fauna, with naticids and neogastropods dominating. An erect, branching sponge is a common element of this fauna, though none appear to be preserved *in situ*. Above this basal carbonate bed is a thin, red-weathering, silt-enriched parting, followed by a harder, less bioturbated shelly bioclastic limestone that contains at its base the large tall-spired gastropod *Campanile* in some abundance, together with *Acteonella*, *Dictyoptychus* and other large molluscs.

Succeeding beds are well-sorted orbitoid-rich bioclastic limestones. These contain little in the way of macrofauna except for a very distinctive horizon of large hippuritid rudists *in situ*, some 4–5 m above the base of the limestone succession.

2. Palaeoenvironmental interpretation. The succession at Jebel Bu Milh commences with quartz sands, gravels and conglomerates representing open-water, nearshore deposits around the newly emergent obduction complex. The succession shallows upwards, with the *Acteonella* conglomerates representing open shore-face, shell-lag accumulations at wave base, and the overlying cross-bedded sands with beached driftwood representing tidal sandbars. The clastic succession is abruptly replaced by carbonate platform deposits, presumably as nearby islands became submerged. A thin deposit of silty bioclastic limestone rich in naticid gastropods represents shallow subtidal sands, possibly formed at wave base in a protected back-bar environment. The presence of the large neritid *Lisocheilus* indicates that shallow rocky substrates lay in the vicinity. The remaining carbonate succession, by comparison with beds at Jebel Rawdah, represent shallow subtidal carbonate sand flats formed above wave base.
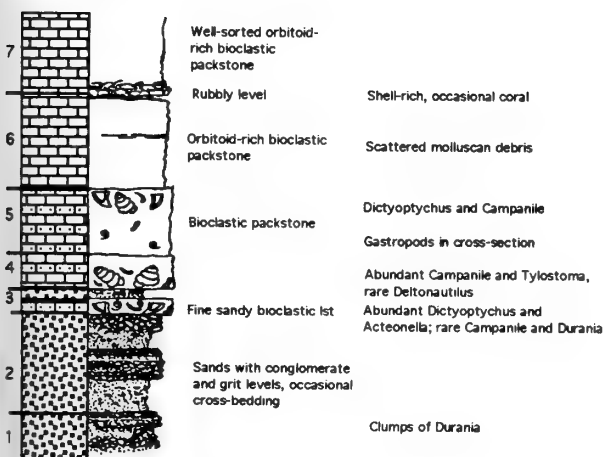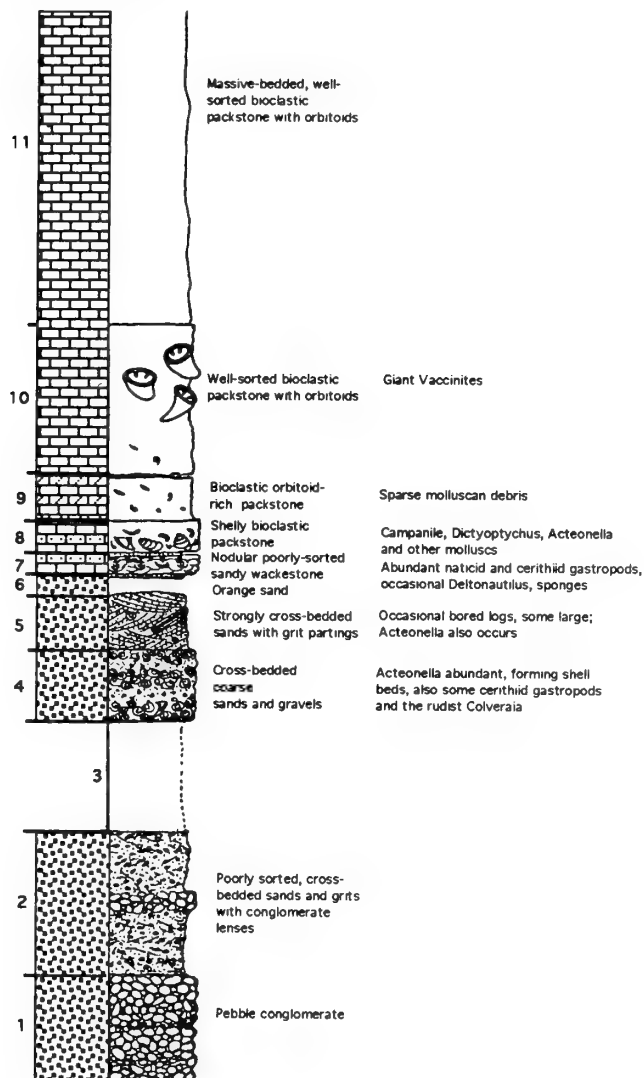
Fig. 9   Measured sections made at Jebel Bu Milh, sections 1 and 2 (see Fig. 3 for locality).

Jebels Buhays, Thanais and Aqabah

1. Lithological succession and faunal assemblages (Fig. 10). These three jebels show virtually the same succession and can therefore be treated together. The initial siliciclastic succession of pebble conglomerates, sands and gravels is thinner than at Jebel Rawdah or Jebel Bu Milh. At Jebel Aqabah the succession commences with a 50 cm well-sorted calcarenite resting directly on top of slightly weathered ophiolite. This basal bed is notable for the small, uniform size of its fossils; a small heteromorph ammonite, *Glyptoxoceras* sp., was recovered from here. Elsewhere the basal contact is not seen. Towards the top of the clastic sequence, at Jebel Buhays, section 1, come 3 to 4 metres of laminar and cross-bedded sands. These contain a fauna of infaunal venerid bivalves and small turreted gastropods.

As elsewhere, there is a sudden elimination of siliciclastics coincident with the onset of biocalcarenite deposition, marking the base of the Simsima Formation. The limestone succession begins with a hard, 80 cm thick, sandy bioclastic shell bed full of the gastropods *Acteonella* and *Campanile*, the echinoid *Goniopygus* and rudist fragments (*Durania* and hippuritid), as well as other molluscan debris. Occasional compound corals occur at this level, but apparently not *in situ*.

The succeeding 3 to 4 metres consist of highly bioturbated, poorly sorted coarse- to medium-grained bioclastic limestones, with scattered orbitoid foraminifera that increase in abundance upwards. These beds are rich in infaunal echinoids (cassiduloids, especially *Pygurostoma*, and the holectypoid *Globator*) as well as small epifaunal regular echinoids. They are also rich in gastropods and bivalves, both infaunal and soft-bottom epifaunal forms. The only rudist to occur here in abundance is the small recumbent *Glabrobournonia*. Within this succession there is a major red-stained, silt-enriched layer that immediately overlies a thin bed of fine, ?dolomitized limestone.

There is then a second major shell-lag deposit, full of large sponge-bored shells of *Acteonella* and other molluscs. Above this the bedding becomes much more massive and the limestones better sorted and cemented. Immediately overlying the *Acteonella* shell bed is an orbitoid-rich packstone with rhodolite bands and a low diversity fauna of the rudist *Dictyoptychus* and the gastropod *Campanile*.

A major red-weathering silt-enriched horizon occurs towards the top of the sequence and is immediately overlain by a one metre thick brown-weathering silty limestone, rich in tall cylindriform hippuritids. Associated here is the echinoid *Codiopsis*, indicative of rocky shore habitats. The silt-enriched bed records a marked increase in the clastic component at this level. It is overlain by massive-bedded, well-sorted carbonate sands/silts with orbitoids.

2. Palaeoenvironmental interpretation. The palaeoenvironmental setting is similar to that seen elsewhere, with shallow marine sands, gravels and conglomerates deposited above active wave base. The basal calcarenite at Jebel Aqabah probably represents a shoreface sand, as suggested by the well-sorted clasts and fossils.

These sands, gravels and conglomerates are replaced abruptly by coarse, poorly sorted bioclastic calcarenites containing a diverse molluscan and echinoid fauna. These beds are highly bioturbated and were deposited in a protected environment below wave-base, possibly in a shallow lagoonal

setting. The occasional large compound coral near the base suggests that reefal patches developed nearby. Periodic minor adjustments in sea-level resulted in red-weathering, silt-enriched partings and beds, marking temporary influxes of fine iron-rich silt-grade clasts while thin dolomitic levels may signify temporary supratidal exposure.

A subsequent regressive phase led to the deposition at wave base of the *Acteonella* shell-lag of bed 11 followed by orbitoid-rich carbonate sands with a low diversity macrofauna. We interpret these well-sorted and well-lithified beds as shallow water platform shoals formed above active wave base. There was a brief event that created the upper iron-rich siltstone band (bed 14) which was followed by a bed with hippurited thickets and the shallow-water echinoid *Codiopsis*, indicative of nearshore conditions. Shallow-water carbonate shoals form the remainder of the succession.

Jebel Faiyah

1. Lithological succession and faunal assemblages (Fig. 11). Here the sequence overlying weathered ophiolite begins with pebble conglomerates, with interspersed grit and sand lenses becoming more common towards the top. Occasional fragments of thick-shelled mollusc are present indicating a marine origin for the unit.

As in other sections, there is an abrupt change to carbonate sedimentation, commencing with a 40–50 cm shell bed full of *Acteonella*, together with lesser amounts of rudist fragments and other thick-shelled molluscan material. The succeeding 3 metres consist of highly bioturbated, poorly-sorted bioclastic limestones, with rhodolites and orbitoid foraminifera, a diverse fauna of gastropods, small regular echinoids and *Dictyoptychus* bands.

There is a major, 10 cm thick, red-coloured, silt-enriched bed which, as at Jebel Buhays, is interpreted as marking a minor change in sea-level with increased erosion of lateritic soils from the hinterland. It is succeeded by *in situ* coral thickets with associated hippuritid rudists (bed 6, section 1a). The majority of *in situ* colonies are erect, branching forms some 50 cm in diameter, with intermixed erect colonies of cylindrical hippuritids. A variety of other colonial corals and rudists also occur. There is also a moderately diverse fauna of small regular echinoids, such as *Glyphopneustes*, and small gastropods at this level.

Next come a few metres of thick-bedded, orbitoid-rich bioclastic limestones with occasional levels of *Dictyoptychus* and rhodolites but little else. There is then a return to red-weathering, poorly sorted bioclastic limestones with a significant silt-grade component (beds 8–10). These beds appear to be relatively iron-rich. The fauna is diverse and dominated by the epifaunal bivalves, *Pycnodonte* and *Agerostrea*. Small discoidal corals (*Cunnolites*), occasional compound corals, the foraminifer *Loftusia* and rudist *Glabrobournonia* all occur at this level.

The succeeding thick sequence of rather massive, well-lithified and well-sorted carbonate sands, rich in orbitoid foraminifera, but with no observable macrofauna, is truncated by an erosion surface.

2. Palaeoenvironmental interpretation. The succession begins with shallow-water sands and gravels deposited above active wave base. In places they may even become intertidal or supratidal (Skelton *et al.* (1990) reported the presence of sedimentary structures indicative of intertidal or supratidal

Jebel Buhays 1

16 — Massive-bedded orbitoid packstone

15 — Brown-weathering, silty fine calcarenite — Codiopsis; occasional Dictyoptychus

14 — Red silty wackestone — Small hippuritids common; Globator rare / Hemiaster / Dictyoptychus

13

Massive-bedded, well-sorted orbitoid packstone with rhodolite bands — Scattered Dictyoptychus

12

11 — Shelly calcarenite — Large Dictyoptychus, Campanile, Tylostoma and Neithea / Acteonella shell lag with Neithea, Bournonia, lophids and Dictyoptychus

10 — Rubbly bedded, poorly sorted, orbitoid-rich bioclastic wackestone with rhodolite bands — Acteonella (small) and other molluscs; occasional Astrogyra; Globator common.

9 — ?dolomitized lst

8 — Rubbly orbitoid-rich wackestone — Campanile, Plagiostoma, Neithea, Scabrotrigonia, rare Dictyoptychus, vermiform gastropod; Phymosoma, Globator

7 — Red silty wackestone

6 — Orange, bioturbated poorly-sorted bioclastic wackestone with some orbitoids and rhodolites — Small Acteonellids and other gastropods; Pycnodonte, Bournonia; Cunnolites; regular echinoids, Globator; decapod claws

5 — — Lyria, strombid gastropods, eligmids, Granocardium, Scabrotrigonia

4 — Sandy bioclastic packstone — Campanile, Acteonella, Crassatella, Pycnodonte, rare Durania fragments; Porosoma

3 — Pebble conglomerate

2 — Calcareous sand with grit and pebble lenses — Mesocallista and small gastropods in lenses

1 — Pebble conglomerate

Jebel Aqabah

5 — Sandy packstone — Acteonella common with much rudist debris and other molluscan material

4 — — Infaunal venerid bivalves common, with low diversity gastropod fauna

3 — Coarse sand/gravel with conglomeratic lenses

2 — Boulder conglomerate

1 — Well-sorted shelly calcarenite packstone — Small shelly fossils including Faujasia and Petalobrissus: Nostoceras

Fig. 10   Measured sections made at Jebel Buhays, sections 1 and Jebel Aqabah (see Fig. 4A for locality).

Jebel Faiyah 1a

11 — Thick-bedded well-sorted packstones with scattered orbitoids and bands of chert nodules

10 — Bioturbated, silty, poorly-sorted wackestone; red-weathering — Pycnodonte, Spondylus, Agerostrea, Amphidote, Dictyoptychus, Cunnolites, Noetlingaster, Loftusia

9 — Rhodolite band

8 — Poorly sorted bioclastic wackestone — Pycnodonte uncinella

7 — Thick-bedded, well-sorted orbitoid-rich packstone with rhodolite bands — Rare Dictyoptychus

6 — Well-sorted, thick-bedded bioclastic packstone with abundant leptorbitolines — Large Dictyoptychus, Noetlingaster

Branching coral thickets with hippuritid colonies

5 — Highly bioturbated red marl-rich wackestone

4 — Dictyoptychus

3 — Orange poorly-sorted bioclastic packstone with scattered orbitoids and some siliciclastic grains — Dictyoptychus, small gastropods, Hattopsis

2 — Well cemented sandy bioclastic packstone with rhodolites — Acteonella, small gastropods, sparse rudists, turritids and callianasid claws

1 — Sands and pebble conglomerates

Jebel Faiyah 1b

8 — Bioclastic packstone with orbitoids

7 — Red silty wackestone — Loftusia, Pycnodonte, bivalves and gastropods; Mimiosalenia, Globator

6 — Orbitoid-rich packstone with occasional rhodolite bands — Occasional molluscan debris

— Dictyoptychus

5 — Bioclastic packstone with orbitoids — Occasional Dictyoptychus

4 — Poorly sorted bioclastic packstone — Branching coral thickets in situ; Hippurites colonies many gastropods; rare Noetlingaster

3 — Reddish marl parting. Fine carbonate sand — Abundant Dictyoptychus and many gastropods and small echinoids

2 — Coarse poorly-sorted bioclastic packstone. Shelly bioclastic packstone — Acteonella abundant at base

1 — Pebble conglomerate with sand lenses

Fig. 11 Measured sections made at Jebel Faiyah, sections 1a and 1b (see Fig. 4A for locality).

environments from these beds). Clastic input ceased suddenly, marking a major transgressive event, and was replaced by carbonate deposition. The carbonate succession began with a transgressive shell-lag deposit rich in acteonellids, after which shallow lagoonal conditions were established for a short period. There was then a minor shift in sea-level, creating a silt-enriched band, which was immediately followed by the establishment of coral-rudist level bottom reefal thickets and peri-reefal bioclastic sands. These in turn were quickly replaced by shallower-water bioclastic carbonate sands with abundant orbitoid foraminifera. These we interpret as shallow-water platform shoals formed above active wave base. Later, a second transgressive phase, marked by an input of siliciclastic material, brought a brief return to deeper water conditions, below active wave base, and the establishment of a more diverse fauna once again. This, however, was short-lived and shallow-water shoal conditions quickly returned with the deposition of massive bedded carbonate sands and the virtual disappearance of benthic fauna.

GENERAL PALAEOENVIRONMENTAL SYNTHESIS

The autochthonous late Cretaceous succession was deposited over a deeply weathered surface of ultrabasic rocks, which must have been exposed subaerially for some time. Initial deposits were locally derived conglomerates and grits formed around the shores of the newly uplifted ophiolite massifs. Pebbles and boulders are well-rounded. Although rudist and acteonellid debris does form a component of these beds, they probably represent shell coquinas washed onshore from subtidal sand-flats rather than autochthonous fauna. There is evidence locally for more sheltered shoreface facies with infaunal bivalves, or for more stable cobble-bottom development, with an *in situ* fauna of encrusting oysters and/or corals. In places, as Skelton *et al.* (1990) note, the rudist *Durania* can be found living *in situ* in cross-bedded sands.

A marine transgression largely drowned these ophiolite islands and led to the onset of carbonate deposition. During this transgression, shoreface reefal debris, with mixed hippuritid and radiolitid rudists and massive compound corals, was deposited as a coarse lag at the base of the transgression. The corals are, for the most part, encrusting forms and are accompanied by a shallow intertidal to immediately subtidal regular echinoid fauna composed of species adapted for life on hard substrata within the zone of active wave surge. Acteonellid gastropods are a characteristic feature of such shell-lag deposits. *Faujasia* is the only common infaunal echinoid in this environment and probably lived in nearshore or shore-face clean, well-washed sediments. Slightly more protected sand beds were colonized by non-siphonate infaunal bivalves such as *Scabrotrigonia* and *Cucullaea*.

This facies was succeeded, as sea-level rose, by a thick succession of rather muddy sands formed at or below active wave base. At some levels the large semi-recumbent rudist *Dictyoptychus* is common, together with bands of rhodolites, dense orbitoid foraminiferal aggregates and abundant small infaunal cassiduloid echinoids (*Petalobrissus* and *Zuffardia*). The sea bottom must have been loose and unconsolidated, lying at or just below active wave base. It regularly received storm-washed bioclastic material.

Elsewhere, solitary discoidal corals and the larger benthic foraminifer *Loftusia* occur in profusion together with pycnodont oysters and a moderately diverse gastropod assemblage in what appears to have been a slightly muddier sand. Infaunal echinoids are more or less absent from this facies, though the small epifaunal regular echinoid *Hattopsis* is often locally abundant and may indicate the presence of algal stands. The molluscan fauna is dominated by gastropods (especially the ?algivore *Acteonella borneensis* and the filter-feeding Umboniidae gen. nov.) and the epifaunal 'Pycnodonte' uncinella. We interpret these beds as stable, possibly algal-bound, sands lying below wave-base. Where this facies occurs close to reefal thickets there is a much higher diversity of regular echinoids accompanied by the holectypoid *Globator*.

Unconsolidated calcarenite shoals, deposited above active wave base, form a major part of the upper succession and contain the lowest faunal diversity. The absence of any large-scale cross-bedding suggests these formed as shallow, broad, subtidal expanses of sand. Rotaline and milioline foraminifera are the predominant bioclasts in this facies, along with dasycladacean algae. It is in this environment that the large selective deposit feeding irregular echinoids *Hemipneustes*, *Pygurostoma* and *Stigmatopygus* are found. The only regular echinoid found to inhabit this environment was *Noetlingaster*.

At Jebel Huwayyah, however, the highest beds appear rather finer grained and contain the infaunal spatangoid echinoid *Proraster*. These may be local basinal sediments deposited below wave base, and possibly represent the deepest water sediments present in the sequence.

The palaeoenvironmental reconstruction that emerges from our combined sedimentological and faunal evidence differs somewhat from that given by Skelton *et al.* (1990). They interpreted the lower part of the Simsima Formation as tidal deposits, whereas we believe that this is inconsistent with both the sedimentological and faunal evidence. The petrography of the sediments indicates deposition below wave base. This is supported by the diverse echinoid fauna, which is also at variance with a tidal environment.

The faunal associations that we recognize represent more-or-less contemporary assemblages that replace one another in vertical succession as a result of shifting sedimentological facies. We found very little stratigraphic variation within single lineages, except in species of the echinoids *Hattopsis* and *Hemipneustes*. Consequently, we believe that the differences in the assemblages reflect variations in palaeoenvironmental conditions over the carbonate platform and represent coexisting communities.

BIOSTRATIGRAPHICAL RESULTS

Maastrichtian biostratigraphic zonation. The Qahlah Formation has been regarded as Campanian or early Maastrichtian in age, and the Simsima Formation as Maastrichtian (e.g. Skelton *et al.* 1990). The boundary between Campanian and Maastrichtian stages has been defined on the basis of a range of biostratigraphic criteria, involving belemnites, ammonites, planktonic foraminifera and coccoliths (amongst other groups). However, recent reviews (Burnett *et al.* 1992, Kennedy *et al.* 1992, Hancock *et al.* 1992) have demonstrated

that these various data do not correspond. Indeed, Obradovich (1993) concluded that the interval between the widely adopted planktonic foraminiferal boundary datum (the extinction point of *Globotruncanita calcarata*) and the widely adopted belemnite definition (appearance of *Belemnella lanceolata*) is at least three million years. There is as yet no agreed definition of the boundary, and subdivisions of the stage into Lower/Upper or Lower/Middle/Upper vary widely between authors. Indeed, in the absence of a clear statement of which definitions of stage and substage limits are used, these terms are near meaningless.

Burnett *et al.* (1992) were able to place the putative markers for the base of the Maastrichtian in sequence, as well as certain other key fossil occurrences. Their scheme is as follows:

(Youngest)
– last occurrence of the nannofossil *Quadrum trifidum* [or *Tranolithus phacelosus* (= *orionatus*)].
– first occurrence of the ammonites *Pachydiscus (P.) neubergicus* and *Acanthoscaphites tridens*.
– last occurrence of the nannofossil *Broinsonia parca*.
– first occurrence of the ammonite *Hoploscaphites constrictus s.l.*
– first occurrence of the belemnite *Belemnella (B.) lanceolata*.
– last occurrence of the ammonite *Nostoceras (N.) hyatti*.
– last occurrence of the nannofossil *Reinhardtites anthophorus* (or *Eiffellithus eximus*).
– first occurrence of the ammonite *Nostoceras (N.) hyatti*.
– last occurrence of the planktonic foraminifer *Globotruncanita calcarata*.
– first occurrence of the planktonic foraminifer *Globotruncana falsostuarti*.
– first occurrence of the nannofossil *Reinhardtites levis*.
(oldest)

As they note, the first occurrence of the belemnite *Belemnella lanceolata* is widely taken to indicate the base of the Maastrichtian stage, and this is the definition adopted in the present work. Birkelund *et al.* (1984), in their review of the conclusions of the 1983 Copenhagen Meeting on Creta-

ceous stage boundaries, noted that it was 'widely accepted to keep the base of the Maastrichtian close to the appearance of *Belemnella lanceolata*, as this datum is so well-defined and widely accepted in the Boreal realm. However, there is a strong need for finer correlation of this boundary level with the succession in the Tethyan Realm possibly by planktonic foraminifera or coccoliths'.

Since the work of Burnett *et al.* and the partial achievement of the needs expressed at the Copenhagen Meeting (see also Schönfeld & Burnett 1991, Kennedy *et al.* 1992, Hancock *et al.* 1992, Hancock and Kennedy 1992) further refinements in correlation of the base of the Maastrichtian in the classic Boreal sense with Tethyan sequences have been achieved through the work of Burnett, Kennedy & Ward (1992), Hancock *et al.* (1993), Hancock & Kennedy (1992) and Ward & Kennedy (1993). These results are summarized in Figure 12. Ward & Kennedy (1993) recognized a threefold ammonite zonation of the Maastrichtian, with a fourth zone of *Pseudokossmaticeras tercense* that was possibly in part Campanian, in part Maastrichtian. Taking the base of the Maastrichtian at the first appearance of *Belemnella lanceolata*, the work of Hancock & Kennedy (1992) and Hancock *et al.* (1992) demonstrate that *Pachydiscus (P.) epiplectus*, *Hoploscaphites constrictus* and *P. (P.) neubergicus* first occur within a very narrow interval, such that the base of the Boreal *lanceolata* Zone and Tethyan *epiplectus* Zone are coeval, within the current limits of biostratigraphic correlation.

For subdivisions of the Maastrichtian we use Lower and Upper Substages, as is widely accepted by workers in the Boreal Realm, the base of the Upper Maastrichtian lying at the base of the *Belemnitella junior* Zone (Fig. 12).

Anapachydiscus fresvillensis (index species of the second zone of the Maastrichtian of Ward & Kennedy 1993) first occurs in the *junior* Zone in the Netherlands (Kennedy 1987). The base of the Boreal *junior* Zone and Tethyan *fresvillensis* Zone are coeval, within current limits of biostratigraphic correlation. *Anapachydiscus terminus*, index of the highest Tethyan Maastrichtian ammonite zone, is now known from the Boreal *casimirovensis* Zone (as *Anapachydiscus* aff. *fresvillensis* of Birkelund 1993 in Denmark, and, subsequently, in the Netherlands (Jagt, in press)). For a more refined division

SUBSTAGE	BOREAL BELEMNITE ZONATION		AMMONITE ZONATION	INOCERAMID ZONATION
Upper Maastrichtian	*Belemnella casimirovensis*		*Anapachydiscus terminus*	
				Trochoceramus morgani
	Belemnitella junior		*Anapachydiscus fresvillensis*	
				Trochoceramus ianjonaensis
Lower Maastrichtian	*Belemnella occidentalis*	*Belemnella fastigata*		
		Belemnella cimbrica	*Pachydiscus (P.) epiplectus*	
		Belemnella sumensis		
	Belemnella lanceolata	*Belemnella obtusa*		*Trochoceramus monticulae/radiosus*
		Belemnella pseudobtusa		
		Belemnella lanceolata		

Fig. 12   Biostratigraphic zonation schemes for the Maastrichtian based on belemnites, ammonites and inoceramid bivalves, and their correlation.

of the Lower Maastrichtian reference will be made to the zonation of Schulz (1979: fig. 12).

Good palaeontological dating and correlation between the isolated jebels is very limited. Within each jebel there is evidence of sedimentation having taken place on an uneven sea-floor and relativily rapid changes of thickness and facies are sometimes visible by casual inspection. Larger benthonic foraminifera are often abundant but apparently controlled in their distribution by palaeoenvironment. Further careful collecting would be necessary before their stratigraphical potential is realized. Therefore, here we use evidence from the ammonite, inoceramid bivalve and echinoid faunas, together with inferred sea-level changes.

Ammonite biostratigraphy. The small number of late Cretaceous ammonites from the United Arab Emirates-Oman borders region (Kennedy, this volume) provide us with some constraints on the age of the succession. More weight has been placed on the pachydiscids than the heteromorphs, largely because they are better preserved.

The sections at Jebel Huwayyah include at least three ammonite horizons. The first and lowest contains an unidentified species of *Pachydiscus*, which was discovered at the top of the sand and conglomerate sequence of the Qahlah Formation, just below the *Loftusia*-rich beds, and only indicates a late Upper Cretaceous age.

The *Loftusia*-rich beds themselves have yielded the greatest number of ammonites, including *Pachydiscus (Pachydiscus) dossantoi* (Maury, 1930), *Lewyites ambindense* (Collignon, 1971), *Nostoceras (Nostoceras) major* Kennedy & Cobban, 1993, *Nostoceras (Nostoceras)* sp., and a *Libycoceras* sp. (not described; photograph only seen). The implied ages of these ammonites are somewhat contradictory. *Pachydiscus (P.) dossantoi* (Maury, 1930) is imprecisely dated within the Maastrichtian but occurs in the highest of three ammonite horizons in the Nkporo Shale of south-eastern Nigeria (Zaborski, 1985). At that locality it is closely associated with the inoceramids *Trochoceramus ianjonaensis* (Sornay) and *Endocostea coxi* (Reyment), which indicate a late Lower Maastrichtian to early Upper Maastrichtian age. *Lewyites ambindense* (Collignon, 1971) is known only from the lower Upper Maastrichtian, *fresvillensis* Zone. *Nostoceras (Nostoceras) major* Kennedy & Cobban, 1993 is Upper, but not uppermost, Maastrichtian, with an inferred *fresvillensis* Zone age. The presence of *Lewyites ambindense* and *Nostoceras (Nostoceras) major* imply a lower Upper Maastrichtian, *fresvillensis* Zone age. However, there are also two species that suggest an earlier age for at least part of the unit; *Nostoceras (Nostoceras)* sp. is uppermost Campanian or lower Lower Maastrichtian in age, and a specimen of *Libycoceras*, now in the Arab Emirates University Museum, has a bifid outer saddle indicative of the earliest of the three *Libycoceras* horizons described by Zaborski (1982) from Nigeria, and a late Campanian age. The age of the *Loftusia*-beds could therefore be as old as late Campanian or as young as early Upper Maastrichtian.

In the northwestern part of the outcrop at Jebel Huwayyah, close to where it is cut by the road, the lower part of the Simsima Formation yielded *Pachydiscus (Pachydiscus) neubergicus neubergicus* (Hauer, 1858), and *Lewyites ambindense* (Collignon, 1971). *Pachydiscus (P.) neubergicus neubergicus* (Hauer, 1858) implies a lower Lower to lower Upper Maastrichtian, *epiplectus* and *fresvillensis* Zones age. As pointed out above, *Lewyites ambindense* (Collignon) is

known only from the lower Upper Maastrichtian.

A specimen of *Desmophyllites diphylloides* (Forbes, 1846) was found in bed 21 at Jebel Rawdah, section 2, well up in the Simsima Formation. However, the species is not age diagnostic, and its known range is Santonian to Upper Maastrichtian, *fresvillensis* Zone, and possibly higher. However, from Jebel Rawdah section 1, from scree almost certainly derived from the top of bed 4, we found a specimen *Brahmaites (Anabrahmaites) vishnu* (Forbes, 1846). The few well-dated specimens of this species are Upper Maastrichtian, *fresvillensis* Zone, and possibly younger in age.

In the basal transgressive calcarenite shell bed beneath the sands and conglomerates of the Qahlah Formation at Jebel Aqabah a *Glyptoxoceras* sp. was recovered. However, the genus is not age diagnostic and ranges from Santonian to upper Upper Maastrichtian. At Jebel Buhays, section 2, a *Libycoceras* sp. was found in the basal conglomerate of the Qahlah Formation. *Libycoceras* species first appear in the Upper Campanian and may range into the Lower Maastrichtian (Zaborski, 1982).

The basal beds of the Simsima Formation at Jebel Buhays, section 1, yielded a specimen of *Pachydiscus (P.) dossantoi* (Maury, 1930) which suggests a 'mid-Maastrichtian' age, presumably not very different to the *Loftusia*-rich beds at Jebel Huwayyah.

In conclusion then, the meagre ammonite data that we have suggests that the basal transgressive sands and conglomerates are late Campanian to 'mid-Maastrichtian' in age, whereas the main carbonate deposits of the Simsima Formation are of early Upper Maastrichtian, *fresvillensis* Zone, age. At Jebel Huwayyah the *Loftusia*-rich horizons may be as old as late Campanian or as young as early Upper Maastrichtian, *fresvillensis* Zone. We do not know whether or not sedimentation continued to the end of the Maastrichtian.

Inoceramid biostratigraphy. Inoceramid biostratigraphy has been based on what appear to be evolving lineages, often expressed as the ranges of subspecies. These are usually defined as the timespan of particular 'morphs' within an evolving species, although short-term biological events, such as the widespread 'flood' of a particular species or subspecies, are also important. Both methods can provide useful biostratigraphical data.

In recent years much progress has been made on integrating biostratigraphic data derived from Upper Cretaceous inoceramids and other fossil groups with data from sequence stratigraphy. Of all the Upper Cretaceous stages, however, the inoceramid biostratigraphic scheme for the Maastrichtian is the least well-established.

Species of the genus *Trochoceramus* hold the most promise for establishing a sound Maastrichtian biostratigraphy, since they apparently represent a relatively simple evolutionary lineage. *Trochoceramus* species have a somewhat rounded shell outline, with their umbones set back from the anterior, and have evenly spaced, rounded, comarginal ribs and distinctive radial ribs. The earliest species is narrow, with a regularly curving shell, but later species have a more convex shell, which is narrow in the early stages, but then undergoes a significant change in coiling direction, markedly increasing the relative volume of the mantle cavity. A similar change is also observed in the earlier genus *Cremnoceramus*.

Here we recognize three successive inoceramid faunas of *Trochoceramus* which can be used to zone the Maastrichtian. The lower division is characterized by the narrow, regularly

curved species *Trochoceramus* cf. *monticulae* (Fugger & Kastner) (?= *Trochoceramus radiosus* (Quaas)). These flat forms first occur in very late Campanian strata (e.g. in the Nacatoch Sand of Navarro County, Texas, U.S.A. (Stephenson 1941, pl. 13, fig. 3), and from Ammoniten Berg in the western Egyptian desert, apparently co-occuring with *Libycoceras ismaeli* (Quaas, 1902). However, the species becomes much more widespread in the lower part of the Lower Maastrichtian (Dhondt, 1983).

The middle division is characterized by a more convex species of *Trochoceramus*, *T. ianjonaensis* (Sornay), its convexity arising from a sharp change in shell curvature following an initial flattish stage. Such forms are known from Madagascar, where they have been dated as 'lower' Maastrichtian (Besairie 1972), although the ammonites listed suggest levels well into the Upper Maastrichtian as defined here. They are also known both from the Calabar district of Nigeria, where they are 'mid'-Maastrichtian, and the St. Lucia Formation of Zululand, Republic of South Africa, where they almost certainly extend into the Upper Maastrichtian. Finally, they are also reported from Libya, but apparently not associated with ammonites.

The upper division is characterized by *Trochoceramus morgani* (Sornay). It is of Upper Maastrichtian age and, so far, has only been recognized from the Calcaire à Baculites of the Cotentin Peninsula, France. *T. morgani* clearly differs from *T. ianjonaesis* by the smaller average size of the initial flat part of the shell (this average is 67% of the average size in *T. ianjonaensis*). Put another way, *T. ianjonaensis* includes forms with large and small initial shells, whereas *T. morgani* includes only specimens with small initial shells. Because the reduction in size of the initial flat portion of the shell has not been recognized in *Trochoceramus* from the Republic of South Africa, it is uncertain whether this size reduction represents a genuine world-wide change in the lineage or simply a geographical variation. A tentative biostratigraphic scheme for the Maastrichtian based on inoceramid bivalves and compared with the cephalopod biochronology is presented in Fig. 12.

Although inoceramid bivalves are proving useful for the division of the Maastrichtian they occur only rarely in the Upper Cretaceous deposits of the U.A.E. and Oman. We have discovered them at only three horizons, and so far only the material from Jebel Rawdah is at all well-preserved. Furthermore, none of this material includes species of *Trochoceramus*.

The lowest horizon includes only a fragment indeterminate at generic level, which was recovered from the conglomerate series below the *Loftusia*-beds at Jebel Huwayyah.

At the second horizon, in the basal transgressive shell bed of the Simsima Formation at Jebel Bu Milh, we found a single large fragmentary specimen of '*Platyceramus*' sp. This genus occurs in some abundance in the Maastrichtian succession of the St Lucia Formation in the Republic of South Africa, where it is common in the Lower Maastrichtian, but also seems to be dominant in the uppermost inoceramid horizon of that formation. A rather poorly preserved fragment of *Endocostea* cf. *bebahoaensis* comes from the *Loftusia*-beds at Jebel Huwayyah. It is not sufficiently well preserved to be dated better than Campanian or Maastrichtian.

The highest of the three levels, some way up the Simsima Formation at Jebel Rawdah, has yielded the most important inoceramid fauna. At Jebel Rawdah, section 1, just below the base of the more massive, well-cemented limestones (base of

bed 5) *Endocostea* (*Cataceramus*) *semaili* sp. nov. occurs. This is most comparable with specimens from Nagoryany, Ukraine, and indicates a 'mid-Maastrichtian' horizon. Drs Skelton and Nolan also collected this species, together with *Endocostea* (*Endocostea*) cf. *coxi*, *Endocostea* sp. and '*Endocostea*' *bebahoaensis*, from the south-western part of the jebel at the same locality and possibly the same horizon as the ammonite *Pachydiscus* (*P.*) *neubergicus neubergicus*. *Endocostea coxi* occurs with *Trochoceramus ianjonaensis* in Nigeria and Zululand, while '*Endocostea*' *bebahoaensis* occurs with the same *Trochoceramus* in Madagascar, but is known to be long-ranging (it occurs in the Upper Maastrichtian at Cotentin, France). The inoceramids from Jebel Rawdah imply an early Upper Maastrichtian age, thus giving support to the age suggested by the ammonites from the same horizon.

Echinoid biostratigraphy. Although useful biostratigraphically for division of late Cretaceous–Palaeocene strata in the Boreal realm, echinoid distribution in Tethyan carbonate sequences is at present too poorly known to provide reliable dating of the succession. Furthermore, the environmental constraints of most species makes them highly restricted in their occurrence, and thus of limited value. However, our work has identified two biostratigraphically useful species lineages, *Hemipneustes* spp. and *Hattopsis* spp.

There are three species of *Hemipneustes* which differ in the relative elevation of the test, sharpness of the anterior sulcus and position of the apical disc. At Jebel Rawdah the lowest beds contain the flattest species, *H. persicus* Cotteau and Gauthier, and this species has a relatively broad and shallow anterior sulcus. Above this level, and possibly co-occurring for a short interval, comes *H. arabicus*, a species that is equally flat in profile but with a narrower and more sharply defined anterior sulcus. Higher beds contain an elevated species of *Hemipneustes*, *H. compressus*, and the relative elevation of the test increases up the succession, so that in the upper half of the Simsima Formation, *Hemipneustes compressus* begins to develop a strong apical elevation and narrower frontal groove, resembling the boreal species *H. striatoradiatus*.

The oldest species, *Hemipneustes persicus*, occurs (as *H. sardanyolae* Vidal) in the late Campanian of Spain. *H. arabicus* is endemic to this area, but the highest species, *H. compressus*, is known from the Maastrichtian of the Mari Hills, West Pakistan, where, unfortunately, the precise dating of the beds remains uncertain. At Jebel Rawdah, the replacement of *H. persicus* by *H. arabicus* seems to take place within the Upper Maastrichtian, according to the evidence of the ammonites and inoceramids.

The second biostratigraphically useful lineage comprises the two species of *Hattopsis*. At Jebel Faiyah, two species succeed one another, with *H. paucituberculatus* predating *H. sphericus*. This is useful for local correlation, since it is *H. paucituberculatus* that occurs at the base of the Simsima Formation at Jebel Buhays and *H. sphericus* that occurs near the base of the Simsima Formation at Jebel Rawdah. This then implies that the base of the Simsima Formation is not strictly contemporaneous between jebels.

Finally, it is noteworthy that the basal bed in the *Loftusia*-rich unit at Jebel Huwayyah yields a distinct suite of echinoids seen at no other jebel, including the holectypoid *Coptodiscus*. *Coptodiscus* is known from the late Campanian of Arabia
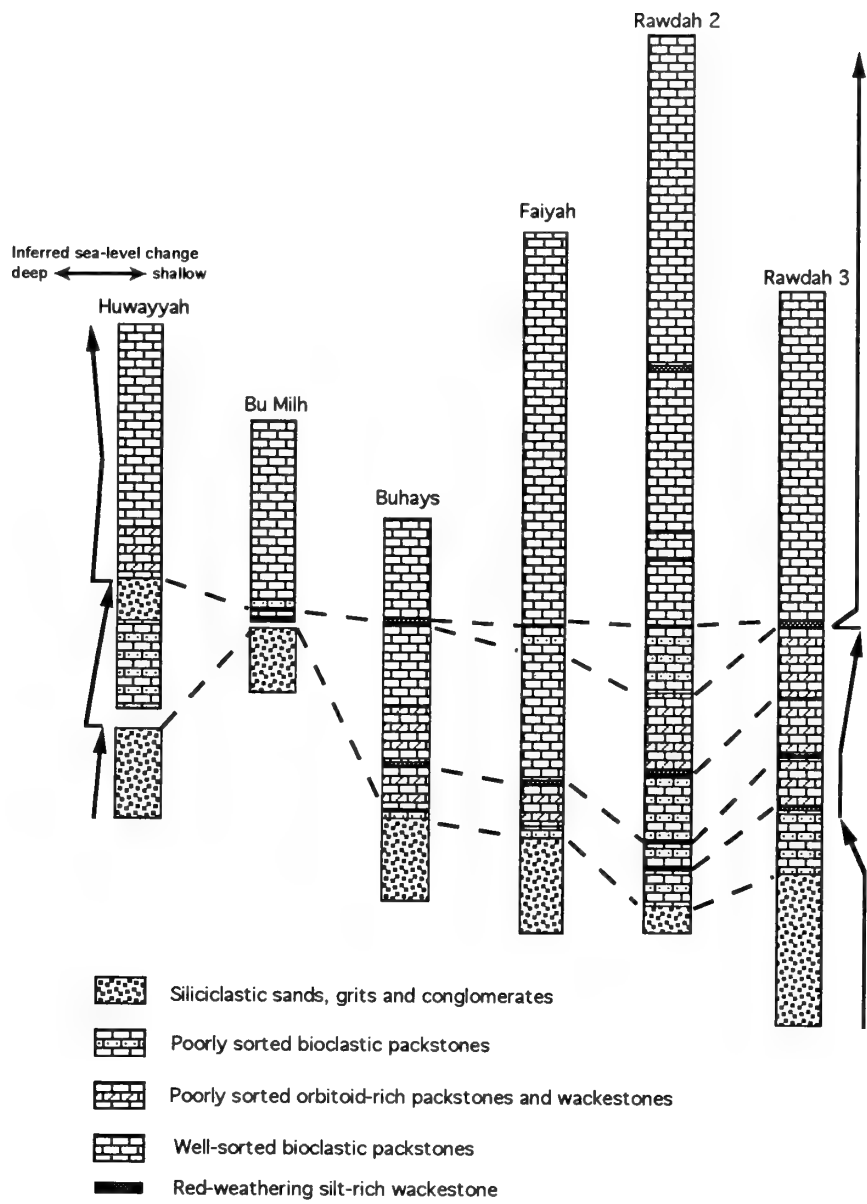
Fig. 13   Tentative correlation between jebels with inferred sea-level curves.

(Kier 1972) and from a presumed similar 'Senonian' horizon in southern Iran.

Global Sea-level curves. In broad terms the stratigraphic successions in the five jebels described here follow the same pattern, but in detail, precise correlation remains difficult, due to rapid shifts in facies and bed thickness across even small areas (Figs 6, 13). Sedimentation upon the Semail Nappe and Hawasina Group follows a typical transgressive pattern, often with massive boulder beds of serpentinite at the base overlain by arenitic and then calc-arenitic sediments, all deposited in shallow or nearshore marine environments. The lower clastic facies of conglomerates, sands and gravels are commonly included in the Qahlah Formation, whereas the sediments above, which are essentially bioclastic cal-carenites, form the Simsima Formation. There is no reason to

suppose, however, that the change from boulder beds and essentially quartz clastics upwards into calcarenites took place at the same time in all the sections we have examined.

The general deepening and shallowing cycles that can be recognized within individual sections allow a means of corre-lation. In all sections the initial coarse clastics of the Qahlah Formation are abruptly terminated, presumably marking the submersion of the ophiolitic complex within the region. This allowed carbonate production to dominate. For most of the Simsima Formation deposition appears to have more-or-less kept pace with subsidence so that sea-level remained around wave-base.

Furthermore, at Jebel Buhays, Jebel Faiyah and Jebel Rawdah there are conspicuous reddened beds and partings that probably contain land-derived iron oxides, which are a common constituent of lateritic soils formed on exposed

ophiolite. These red partings and thin beds presumably formed when lateritic soils were eroded and periodically flushed out to sea in run-off after heavy rains. Some may mark minor fluctuations in sea-level. They are potentially traceable over a wide area and may be important for local correlation. The problem is that there are not the same number of iron-enriched bands currently recognized in the different sections, and it becomes problematic as to which of several alternative bands should be correlated. A tentative correlation is presented in Fig. 13. However, mineralogical and geochemical analyses of these bands is needed to establish whether any have distinctive signatures.

The Cretaceous part of the section at Jebel Rawdah is topped by a limestone conglomerate apparently made up of eroded fragments of the Simsima Formation and including large chunks of rudists. This is in turn overlain by Lower Tertiary limestones. The lack of rounding and poor sorting of the clasts in the limestone conglomerate are probably indicative of subaerial erosion and deposition but we have no way of more accurately dating this period of emergence. It lies somewhere between late Maastrichtian and early Tertiary.

Flexer & Reyment (1989) identified two late Cretaceous transgressive events affecting the Arabo-Nubian shield: one in the late Campanian–early Maastrichtian, and the other in the late Maastrichtian. Although local tectonic events, associated with the ophiolite emplacement, may have had a profound effect on the local sea-level signature, it is tempting to associate the initial submergence of the ophiolitic islands and the sands and conglomerates of the Qahlah Formation with the late Campanian–early Maastrichtian transgression, and the later flooding of these beds and initiation of carbonate platform deposition with the second of these major sea-level transgressions in the late Maastrichtian. The end of the Cretaceous saw a major drop in sea-level.

Summary. Combining the evidence from ammonites, inoceramid bivalves, echinoids and global sea-level curves we conclude that the basal siliciclastic beds of the Qahlah Formation are of latest Campanian age. At Jebel Huwayyah, the *Loftusia*-rich levels of the Qahlah Formation probably encompass Lower to early Upper Maastrichtian. Finally, the Simsima Formation appears to be early Upper Maastrichtian, *fresvillensis* Zone or later.

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APPENDIX

Macrofossils collected in the United Arab Emirates/Oman border region. Echinoids identified by A.B. Smith, nautiloids, bivalves and gastropods by N.J. Morris, P.W. Skelton and R.J. Cleevely, ammonites by W.J. Kennedy, corals by J. Darrell and B.R. Rosen, bryozoans by P.D. Taylor and brachiopods by E.F. Owen. Locality details are given in the main text: bed numbers refer to those shown in figures 5–11. Numbers in square brackets after each name refer to the number of specimens collected.

Jebel Buhays, Section 1

Top of Bed 4. Echinoids: *Arnaudaster cylindriformis* sp. nov. [1]; *Circopeltis? emiratus* sp. nov. [1]. **Ammonite:** *Pachydiscus dossantoi* (Maury) [1].

Bed 10. Echinoids: *Hemipneustes* sp. [1]; *Coenholectypus* cf. *baluchistanensis* (Noetling) [1].

Bed 11. Bivalves: *Dictyoptychus morgani* (Douvillé) [2]; **Gastropods:** *Acteonella crassa* (Dujardin) [6].

Bed 12, base. Echinoids: *Goniopygus arabicus* sp. nov. [1]; *Hattopsis paucituberculatus* sp. nov. [1 fragment]. **Coral:** *Hydnophoraraea* sp. [1]. **Bivalves:** *Scabrotrigonia* sp. [3].

Bed 15. Echinoid: *Codiopsis lehmannae* sp. nov. [1]. **Bivalve:** *Hippurites* cf. *cornucopiae* Defrance [6].

Lowest part of Simsima Formation (beds 4–10) – mostly collected loose. **Echinoids:** Rhabdocidarid, gen. et sp. indet. [1]; *Prionocidaris morgani* (Gauthier) [2]; cidarid spines [2]; *Heterodiadema buhaysensis* sp. nov. [2]; *Orthopsis miliaris* (d'Archiac) [10]; *Salenia nutrix* Peron & Gauthier [5]; *Goniopygus arabicus* sp. nov. [22]; *Glyphopneustes hattaensis* Ali [41]; *Hattopsis paucituberculatus* sp. nov. [11]; *Noetlingaster paucituberculatus* (Noetling) [3]; *Phymosoma hexoaporum* Lambert [13]; *Actinophyma spectabile* Cotteau & Gauthier [4]; *Plistophyma asiaticum* Gauthier [3]; *Circopeltis? emiratus* sp. nov. [1]; *Coenholectypus inflatus* (Cotteau & Gauthier) [8]; *Coenholectypus* cf. *baluchistanensis* (Noetling) [3]; *'Globator' bleicheri* (Thomas & Gauthier) [96]; *Conulus douvillei* (Cotteau & Gauthier) [19]; *Vologesia rawdahensis* Ali [3]; *Pygurostoma morgani* Cotteau & Gauthier [26]; *Petalobrissus* cf. *setifensis* (Cotteau) [1]; *Nucleopygus magnus* sp. nov. [27]; *Arnaudaster cylindriformis* sp. nov. [5]; *Hemipneustes* sp. indet. (fragments) [3]; *Hemiaster hattaensis* Ali [4]. **Bivalves:** *Arca* sp. [1, bivalved]; *Cucullaea* sp. A [3, 2 bivalved]; *'Modiolus'* cf. *capitatus* Zittel [3, bivalved]; *Mytilus* sp. nov? [1, bivalved]; *Modiolus* aff. *typicus* Forbes [3, bivalved]; *Neithea regularis* (Schlotheim) [33]; *Spondylus* sp. C [1]; *Spondylus* sp. D [1]; *Ctenoides* aff. *scaberrima* (Stolizcka) [14]; *?Osculopha* sp. [1]; *?Gyropleura* sp. [1]; *?Pycnodonte uncinella* (Leymerie) [8]; *Amphidonte pyrenaicum* (Leymerie) [2]; *Agerostrea ungulata* (Schlotheim) [4]; Eligmidae [6,

bivalved]; *?Tellinella* sp. [1]; *Glabrobournonia arabica* Morris & Skelton sp. nov. [12]; Tancrediidae cf. *Tatella* sp., sp. nov. [1]; *Clavagella* cf. *semisulcata* Forbes [2, bivalved]; *Pholadomya* sp. B [1, bivalved]. **Gastropods:** *Bathrotomaria* cf. *verdachellensis* (Forbes) [2]; *Calliomphallus* sp. [1]; *Angaria* sp. [1]; *'Tectus'* ex. gr. *rozeti* (d'Archiac) [7]; Umboniinae nov. gen. [9]; *?Rhabdoconcha* sp. [1]; Turritellidae [2]; *Pyrazus* sp. [1]; *Campanile* sp. [8]; *Tylostoma incerta* (Forbes) [9]; Naticidae [1]; Strombidae, gen. nov., cf. *crassicostatus* (Noetling) [1]; Strombidae, gen. nov. [1]; Strombacea [3]; *?Ovula expansa* d'Archiac & Haime [4]; Cypraeidae [1]; *?Tonnacea* [1]; *'Volutilithes' dubia* Noetling [7]; *?Volutoderma* sp. [4]; *Caricella* sp. [1]; Volutidae A [1]; Volutidae B [2]; Volutidae C [2]; Volutidae D [3]; Neogastropoda indet. [1]; *Acteonella crassa* (Dujardin) [4]; *Acteonella caucasica* Zekeli cf. *styriaca* Kollman [3]; *Acteonella* sp. cf. *A. borneensis* Nuttall & Leong [19]; *Acteonella caucasica* Zekeli subsp. nov. [7]; *Acteonella crassa* (Dujardin) [9]; *Neocylindrites* cf. *minutus* Sohl [3]; *Neocylindrites* sp. [1]; opisthobranch [2]. **Corals:** *Polytremacis* sp. [2]; *Aspidastraea* sp. [1]; *Cunnolites* sp. [4]; *Diploctenium* sp. [3]; *Hydnophoraraea* sp. [2]; *Paraplacocoenia orbignyana* (Reuss) [1]; cerioid colony [1]; phaceloid colony [1]; solitary form [1]. **Stromatoporoid:** massive stromatoporoid (bored by bivalves) [1]. **Sponge:** chaetetid [1]. **Bryozoan:** *'Onychocella'* sp. [1]. **Decapod crustaceans:** *Carcineretes* sp. [3 carapaces, 5 limb segments]; crab carapace, species A [1]; crab carapace, species B [2]; claw, indet. [1].

Jebel Buhays Section 1a

Small hill 150 m to south of Jebel Buhays 1. Collected from scree, in rock fall from lowest 4 m of Simsima Formation (beds are steeply dipping and all loose material must be derived from the basal beds here).

Echinoids: *Heterodiadema buhaysensis* sp. nov. [1]; *Orthopsis miliaris* (d'Archiac) [7]; *Salenia nutrix* Peron & Gauthier [2]; *Goniopygus arabicus* sp. nov. [7]; *Glyphopneustes hattaensis* Ali [9]; *Phymosoma hexoaporum* Lambert [3]; *Actinophyma spectabile* Cotteau & Gauthier [1]; *Plistophyma asiaticum* Gauthier [3]; *Coenholectypus inflatus* (Cotteau & Gauthier) [3]; *'Globator' bleicheri* (Thomas

& Gauthier) [occurs]; *Conulus douvillei* (Cotteau & Gauthier) [occurs]; *Vologesia rawdahensis* Ali [2]; *Petalobrissus linguiformis* (Peron & Gauthier) [1]; *Nucleopygus magnus* sp. nov. [9]; *Hemipneustes* sp. [1]; *Hemiaster hattaensis* Ali [3]. **Bivalves:** *Cucullaea* sp. A [4]; *Barbatia* sp. [1]; *Lyriochlamys ternatus* (Münster) [6]; *Neithea regularis* (Schlotheim) [6]; *Agerostrea ungulata* (Schlotheim) [4]; ?*Pycnodonte uncinella* (Leymerie) [1, bivalved]; *Scabrotrigonia* sp. [8]; *Dictyoptychus morgani* Douvillé [1, lid]; *Glabrobournonia arabica* Morris & Skelton sp. nov. [2]; *Clavagella* cf. *semisulcata* Forbes [2]. **Gastropods:** *Tylostoma incerta* (Forbes) [2]; ?Strombidae, gen. nov. [1]; *Pseudomelania [Trajanella]* sp. cf. *conica* (Stolizcka) [2]; *Acteonella crassa* (Dujardin) [13]; *Acteonella* cf. *laevis laevis* (Sowerby) [6]; *Acteonella* cf. *borneensis* Nuttall and Leong [4]; *Neocylindrites* sp. cf *minutus* Stolizcka [1]. **Cephalopods:** *Cimomia* aff. *sowerbyana* (d'Orbigny) [1]; *Deltoidonautilus salisfilius* sp. nov. [1]. **Corals:** *Polytremacis* sp. [1]; *Favia* sp. cf. '*Diplocoenia*' *klogsdorfensis* Trauth [1]; *Barysmilia irregularis* (Reuss) [1]; *Cunnolites* sp. [1]; *Diploctenium* sp. [1]; cerioid colony [1]. **Sponge** [1].

Jebel Buhays 2

Collections made from the scree-slope. Here the bedding is very steep and material is derived from the lowest few metres of section only.

Echinoids: *Salenia nutrix* Peron & Gauthier [1]; *Goniopygus arabicus* sp. nov. [4]; *Coenholectypus inflatus* (Cotteau & Gauthier) [1]; '*Globator*' *bleicheri* (Thomas & Gauthier) [3]; *Conulus douvillei* (Cotteau & Gauthier) [3]; *Pygurostoma morgani* Cotteau & Gauthier [2]. **Bivalves:** *Dictyoptychus morgani* (Douvillé) [1]; *Glabrobournonia arabica* Morris & Skelton, sp. nov. [16]; **Ammonite:** *Libycoceras* sp. [1].

Jebel Buhays 3

Basal limestone (lowest 1m). Echinoids: *Goniopygus arabicus* sp. nov. [4]; *Nucleopygus magnus* sp. nov. [1].

Above first major red-weathering siltstone level. Echinoids: *Circopeltis emiratus* sp. nov. [2].

Loose. Echinoids: *Salenia nutrix* Peron & Gauthier [2]; *Hattopsis paucituberculatus* sp. nov. [2]; *Phymosoma hexoaporum* Lambert [1]; '*Globator*' *bleicheri* (Thomas & Gauthier) [1]. **Bivalves:** *Hippurites cornucopiae* Defrance [1]; ?*Biradiolites* aff. *baylei* Toucas [2].

Jebel Thanais

Lowest 4 m of Simsima Formation. Echinoids: *Heterodiadema buhaysensis* sp. nov. [1]; *Orthopsis miliaris* (d'Archiac) [1]; *Salenia nutrix* Peron & Gauthier [2]; *Goniopygus arabicus* sp. nov. [2]; *Glyphopneustes hattaensis* Ali [6]; *Hattopsis* sp. [1]; *Phymosoma hexoaporum* Lambert [3]; *Plistophyma asiaticum* Gauthier [2]; *Coenholectypus* cf. *baluchistanensis* (Noetling) [2]; '*Globator*' *bleicheri* (Thomas & Gauthier) [5]; *Conulus douvillei* (Cotteau & Gauthier) [8]; *Vologesia rawdahensis* Ali [1]; *Pygurostoma morgani* Cotteau & Gauthier [1]; *Nucleopygus magnus* sp. nov. [4]; *Hemiaster hattaensis* Ali [1]. **Bivalves:** ?*Barbatia* sp. A, cf. *B. morgani* (Douvillé) [2, bivalved]; '*Modiolus*' aff. *typicus* Forbes [1, bivalved]; *Neithea regularis* (Schlotheim) [2]; *Pycnodonte vesicularis* (Lamarck) [1, bivalved]. **Gastropods:** *Acteonella* sp. cf. *A. borneensis* Nuttall & Leong [1]; *Acteonella caucasica* Zekeli subsp. cf. *styriaca* Kollman [1]; *Acteonella caucasica caucasica* Zekeli [1]. **Corals:** *Cunnolites* sp. [1]; *Diploctenium* sp. [1]; *Moltkia isis* Steenstrup [1]; *Paraplacocoenia orbignyana* (Reuss) [1]; coarse meandroid colony [1]. **Bryozoan:** '*Onychocella*' sp. [1]. **Decapod crustacean:** limb segments [3].

Upper beds (equivalent to bed 15 of Jebel Buhays 1). Bivalves: *Hippurites cornucopiae* Defrance [1].

Loose in scree. Bivalves: *Cucullaea* sp. A [2 ,1 bivalved]; '*Modiolus*'

aff. *typicus* Forbes [1, bivalved]; *Chlamys dujardeni* (Roemer) [1]; *Neithea regularis* (Schlotheim) [3]; *Spondylus* sp. E [1]; *Ctenoides* aff. *scaberrima* (Stolizcka) [2]; ?*Amphidonte* cf. *pyrenaicum* (Leymerie) [1]; ?*Osculopha* sp. [1]; Lucinidae gen. indet., sp. B [1, bivalved]; *Dictyoptychus morgani* (Douvillé) [1]; *Glabrobournonia arabica* Morris & Skelton, sp. nov. [1]; *Colveraia variabilis* Klinghardt [1]; *Vaccinites vesiculosus* (Woodward) [4]; *Lapeirousia* sp. [2]; *Pholadomya* sp. B [1, bivalved]. **Gastropods:** *Tylostoma incerta* (Forbes) [1]; *Acteonella crassa* (Dujardin) [5].

Jebel Aqabah

Excellent outcrop of the basal part of the marine sequence resting directly on serpentinized ultramafics.

Bed 1. Echinoids: *Hattopsis paucituberculatus* sp. nov. [1]; '*Globator*' *bleicheri* (Thomas & Gauthier) [2]; *Faujasia eccentripora* Lees [6 juveniles]. **Ammonite:** *Glyptotoxoceras* sp. [1].

Loose. Bivalves: ?*Pycnodonte uncinella* (Leymerie) [2]; *Dictyoptychus morgani* (Douvillé) [1]; ?*Biradiolites* aff. *baylei* Toucas [3]. **Gastropods:** *Acteonella crassa* (Dujardin) [2]. **Cephalopod:** *Cimomia* aff. *sowerbyana* (d'Orbigny) [1]. **Coral:** *Cunnolites* sp. [1].

Jebel Huwayyah, Section 1

Bed 1. Bivalves: ?*Acutostrea* sp. [*ca.* 10].

Bed 3. Bivalves: ?*Acutosrea* sp. [abundant].

Bed 7. Stromatoporoid [1].

Bed 9. Echinoids: *Faujasia eccentripora* Lees [6]; *Hemiaster* sp. cf. *H. hattaensis* Ali [1]. **Bivalves:** *Spondylus* sp. A [1]; *Vaccinites vesiculosus* (Woodward) [5]; ?*Granocardium* sp. [1]. **Gastropods:** ?*Tectus* sp. [1]; *Campanile* sp. [1]; *Amauropsina* aff. *bulbiformis* (J. de C. Sowerby) [1]; '*Ampullina* aff. *splendida*' (Deshayes) [3]. **Corals:** *Cunnolites* sp. [4]; cerioid colony (with *Lithophaga* borings) [1]. **Ammonite:** *Pachydiscus* sp. [1].

Beds 10–11. Echinoids: *Faujasia eccentripora* Lees [33]; *Hemiaster* sp. cf. *H. hattaensis* Ali [1]. **Bivalves:** *Endocostea* cf. *bebahoaensis* (Sornay) [1]; *Spondylus* sp. A [2]; *Plicatula hirsuta* Coquand [4]; ?*Acutostrea* sp. [6]; *Glabrobournonia arabica* Morris & Skelton, sp. nov. [1]; *Pholadomya?* sp. B [1]. **Gastropods:** cf. *Tylostoma incerta* (Forbes) [1]. **Corals:** *Cunnolites* sp. [2]; *Paraplacocoenia orbignyana* (Reuss) [1]; large trochoid solitary [1]; large flabellate solitary [1]; cerioid colonies (5 genera) [7]. **Ammonites:** *Pachydiscus dossantoi* (Maury) [1]; *Lewyites ambindense* (Collignon) [1]; *Nostoceras (Nostoceras) major* Kennedy & Cobban [1].

Beds 9–11 undifferentiated. Bivalves: *Torreites sanchezi* (Douvillé) [2] *Durania* form A [1].

Bed 13. Bivalves: *Durania* spp. [fragments].

Beds 14/15. Echinoids: *Coenholectypus inflatus* (Cotteau & Gauthier) [1]; '*Globator*' *bleicheri* (Thomas & Gauthier) [54]; *Pygurostoma morgani* Cotteau & Gauthier [3]; *Hemipneustes* sp. [1]. **Bivalves:** *Cucullaea* sp. A [1]; *Lyriochlamys ternatus* (Münster) [7]; *Neithea regularis* (Schlotheim) [8]; *Spondylus* sp. A. [2]; *Dictyoptychus morgani* (Douvillé) [1]. **Gastropods:** *Execochirsus* sp. [1]; *Campanile* sp. [1]; Cerithiidae [1]; *Tylostoma incerta* (Forbes) [6]; Strombacea [1]; ?Aporrhaidae [1]; Neogastropods [2]. **Ammonite:** *Pachydiscus dossantoi* (Maury) [1]. **Coral:** *Cunnolites* sp. [1].

Bed 16. Bivalves: *Pycnodonte vesicularis* (Lamarck) [2]; *Agerostrea ungulata* (Schlotheim) [12, bivalved].

Bed 17. Bivalves: *Lyriochlamys ternatus* (Münster) [1]; *Neithea regularis* (Schlotheim) [2]; *Scabrotrigonia* sp. [4]; *Durania* sp. [2]. **Gastropods:** *Bathrotomaria* sp. [1].

Bed 18, towards top of section. **Echinoids:** *Proraster geayi* Cottreau [7].

Loose. Echinoid: *Mecaster* sp.? [1]. **Bivalve:** ?'*Inoceramus*' sp. [1].

Jebel Huwayyah, Section 2

Bed 1. **Echinoids:** *Glyphopneustes hattaensis* Ali [1]; *Coptodiscus magniproctus* sp. nov. [2].

Beds 3–5. **Echinoids:** cidarid spine [1]; *Orthopsis* sp. [1]; *Salenia microprocta* sp. nov. [1]; *?Hattopsis* sp. [1]; *Faujasia eccentripora* Lees [1]; *Hemiaster* sp. cf. *H. hattaensis* Ali [3]; *Mecaster* sp. [4]; *Proraster geayi* Cottreau [2]. **Bivalves:** *Dictyoptychus morgani* (Douvillé) [1]; **Corals:** *Cunnolites* sp. [27]; *Diploctenium* sp. [4]; *Placosmilia* sp. [22]. **Bryozoans:** cf. *Euritina lata* Canu [1]; '*Wilbertopora*' sp. [1]. **Decapod crustacean:** pincer [1]. **Brachiopods:** terebratulid gen. et sp. nov. [3]. **Ammonite:** *Nostoceras* sp. [1].

Bed 7. **Bivalves:** *Vaccinites vesiculosus* (Woodward); **Corals:** *Actinacis* sp. [3]; *Cladocora ?humilis* (Michelin) [7]; *?Aspidastraea* sp. [1]; *Astraraea* sp. [3]; *Calamophylliopsis simonyi* (Reuss) [1]; *Paraplacocoenia orbignyana* (Reuss) [1]; cerioid colonies (3 genera) [4]; thamnasteroid colonies [4]; coarse meandroid colonies [5]; elongate-oval flat solitary corals [3]; flabellate solitary corals [2]; turbate solitary corals [10]; cylindrical solitary corals [3]. **Ammonite:** *Neancycloceras* sp. [1].

Loose in scree, but derived from Loftusia beds, beds 2–7 unless otherwise stated. **Echinoids:** *Prionocidaris?* *emiratus* sp. nov. [1]; *Coenholectypus inflatus* (Cotteau & Gauthier) [3] (probably derived from Simsima Formation above?). **Bivalves:** *Endocostea* cf. *bebahoaensis* (Sornay) [1]; *Lyriochlamys ternatus* (Münster) [8]; *Neithea regularis* (Schlotheim) [19]; *Neithea (Neithella) notabilis* (Munster) [1]; *Spondylus* sp. A [49, 19 bivalved]; *Spondylus* sp. B [12, 4 bivalved]; *Plicatula hirsuta* Coquand [23]; *?Osculopha* sp. [4, 1 bivalved]; *Amphidonte pyrenaicum* (Leymerie) [10, 2 bivalved]; *Agerostrea ungulata* (Schlotheim) [1, bivalved]; *?Eligmidae* indet. [1]; *Ctenoides* sp. [2]; *Chama noetlingi* [7]; *Biradiolites* aff. *baylei* Toucas [1]; *Glabrobournonia arabica* Morris & Skelton, sp. nov. [10]; *Semailia smithi* Morris & Skelton, sp. nov. [1]; *Vaccinites vesiculosus* (Woodward) [25]; *Pholadomya* sp. A, cf. *indica* Noetling [2]; *Pholadomya* sp. B [1, bivalved]. **Gastropods:** *?Angaria* sp. [5]; Turbinidae sp. [5]; Turritellidae sp. [10]; *?Pyrazus* sp. [3]; Cerithiidae sp. [1]; *?Perrisoptera* sp. [7]; *?Naticidae* sp. [7]; *?Fasciolariidae* sp. [1]; Volutidae sp. A [1]; Volutidae sp. B [1]; *?Mitridae* sp. [1]; neogastropods [2]; *Acteonella* sp. [1].

Jebel Rawdah, Section 1

Bed 2. **Echinoid:** *Petalobrissus* cf. *setifensis* (Cotteau) [1]. **Bivalves:** *?'Modiolus'* cf. *capitatus* Zittel [1, bivalved]; *Cucullaea* sp. A [11]; *Lyriochlamys ternatus* (Münster) [2]; *Neithea regularis* (Schlotheim) [7]; *Pycnodonte vesicularis* (Lamarck) [1]; *?Pycnodonte uncinella* (Leymerie) [7]; *Agerostrea ungulata* (Schlotheim) [1]; Indet. ribbed oyster [1]; *Scabrotrigonia* sp. [62, 7 bivalved]; *Durania* spp. [2]; *Glabrobournonia arabica* Morris & Skelton [4]; Tancrediidae, cf. *Tatella*, sp. nov. [2, bivalved]. **Gastropods:** *Acteonella* sp. cf. *borneensis* Nuttall & Leong [4]. **Corals:** *Cunnolites* sp. [7]; *Diploctenium* sp. [1].

Bed 3 (lower part) and top of Bed 2. **Echinoids:** *Orthopsis miliaris* (d'Archiac) [2]; *Salenia nutrix* Peron & Gauthier [2]; *Hattopsis sphericus* Ali [19]; *Noetlingaster paucituberculatus* (Noetling) [5, fragments]; *Coenholectypus* cf. *baluchistanensis* (Noetling) [1]; '*Globator*' *bleicheri* (Thomas & Gauthier) [49]; *Faujasia eccentripora* Lees [5]; *Zuffardia morgani* (Cotteau & Gauthier) [4]; *Petalobrissus* cf. *setifensis* (Cotteau) [17]; *Phymechinus?* sp. [fragment]. **Bivalves:** *?Barbatia* sp. A, cf. *B. morgani* Douvillé [1, bivalved]; *Cucullaea* sp. A [4, 3 bivalved]; *?'Mytilus' nitens* Forbes [1, bivalved]; '*Modiolus*' cf. *capitatus* Zittel [5, 4 bivalved]; *Pinna* sp. [3]; *Endocostea (Selenoceramus) semaili* sp. nov. [1]; *Lyriochlamys ternatus* (Münster) [3]; *Neithea regularis* (Schlotheim) [23]; Limidae [1]; *Plicatula hirsuta* Coquand [1]; *Pycnodonte vesicularis* (Lamarck) [6]; *Pycnodonte vesicularis* (Lamarck) var. *hippopodium* Nillson [1]; *?Pycnodonte uncinella* (Leymerie) [10, 4

bivalved]; *?Amphidonte* cf. *pyrenaicum* (Leymerie) [2]; *Scabrotrigonia* sp. [6, 2 bivalved]; Lucinidae sp. [1]; *?Plagyoptychus* sp. [1]; *Dictyoptychus morgani* (Douvillé) [10]; *Glabrobournonia arabica* Morris & Skelton, sp. nov. [22]; *Durania* spp. [6 fragments]; ?Trapeziidae [1]; *?Mesocallista* sp. [5, bivalved]; Tellininae [1]; ?Tancrediidae, cf. *Tatella*, sp. nov. [2]; *Clavagella* cf. *semisulcata* Forbes [6]; *?Brechites* cf. *aspergilloides (Forbes)* [1]; *Pholadomya* sp. B [1]. **Gastropods:** *Calliomphalus* sp. [4]; *?Angaria* sp. [2]; *?Tectus* sp. [3]; *?Pseudoliotina* sp. [1]; *?Umboniinae*, gen. nov. [64]; euomphalid gen. nov. [6]; *?Rhabdoconcha* sp. [1]; ?Turritellidae [2]; Vermetidae or Siliquariidae [1]; Cerithiidae [7]; Cypraeidae, sp. [4]; *?Cypraeidae*. [3]; *?Volutacea* [1]; *Ampullina* aff. '*splendida*' (Deshayes) [4]; *Tylostoma incerta* (Forbes) [2]; Mesogastropod [2]; *?Anchura* sp. [3]; *?Aporrhaidae* [1]; Hipponicidae [3]; *?Fasciolariidae* [1]; *?Volutidae* [16]; *?Buccinacea* [7]; *Lyria* sp. [8]; *?Lyria* sp. [2]; *Acteonella* sp. cf. *borneensis* Nuttall & Leong [30]; *Acteonella laevis laevis* (J. de C. Sowerby) [1]; *Acteonella* sp. [4]; *Neocylindrites* sp. [2]; oliviform opisthobranch [1]; *?Scaphander* sp. [1]; bullaeform opisthobranchs [2]; elongate opisthobranch [1]. **Cephalopods:** *Cimomia* cf. *sowerbyana* (d'Orbigny) [1]; *Brahmaites (Anabrahmaites) vishnu* (Forbes) [1]. **Corals:** *Cunnolites* sp. [42]; *Diploctenium* sp. [9]; *Aspidastraea* sp. [2]. **Decapod crustacean:** pagurid claw [1].

Bed 3 (upper part). **Echinoids:** *Hattopsis sphericus* Ali [3]; phymosomatid fragment [1]; *Conulus douvillei* (Cotteau & Gauthier) [1]; *Zuffardia morgani* (Cotteau & Gauthier) [1]; *Hemipneustes* sp. [3, fragments]. **Bivalves:** *?Chlamys* sp. [1]; *?Ctenoides* sp. [1]; Cardiidae [3]; *?Fragum* sp. [2]. **Gastropods:** *?Umboniinae*, gen. nov. [6]; *?Rhabdoconcha* sp. [2]; *Campanile* sp. [1]; *?Cerithiidae* indet. [3]; *?'Ampullina* aff. *splendida*' (Deshayes) [1]; *?Tylostoma incerta* (Forbes) [4]; *?Naticidae* sp. [2]; Cypreidae spp. [3]; *Lyria* sp. [2]; elongate, fusiform genus [1].

Bed 4. **Echinoids:** *Glyphopneustes hattaensis* Ali [1]; *Hattopsis sphericus* Ali [15]; *Hemipneustes arabicus* Ali [3]. **Bivalves:** *Neithea* sp. [1]; *Durania* form B [1]; *?Pycnodonte uncinella* (Leymerie) [7]; cf. *Fragum* sp. [3]. **Gastropods:** *?Angaria* sp. [1]; *?Trochacea*, euomphalid gen. nov. [3]; *?Umboniinae*, gen. nov. [4]; Turritellidae [1]; *?Cerithiidae*, sp. [2]; Cypraeidae, sp. [1]; *Caricella* sp. [2]. **Cephalopod:** *Cimonia* aff. *sowerbyana* (d'Orbigny) [1]. **Decapod crustacean:** small spinose pincers [2].

Bed 4 (top). **Echinoids:** *Salenia nutrix* Peron & Gauthier [2]; *Hattopsis sphericus* Ali [29]; *Noetlingaster emiratescus* Ali [1]; *Noetlingaster* sp. [1, fragment]; *Phymechinus perplexus* sp. nov. [2]; '*Globator*' *bleicheri* (Thomas & Gauthier) [15]; *Faujasia eccentripora* Lees [2]; *Hemipneustes persicus* Cotteau & Gauthier [1, fragment]. **Bivalves:** *?'Mytilus' nitens* Forbes [1, bivalved]; '*Modiolus*' aff. *typicus* Forbes [2, bivalved]; *Endocostea (Selenoceramus) semaili* sp. nov. [2]; *Neithea* sp. [6]; *?Pycnodonte uncinella* (Leymerie) [16]; *Scabrotrigonia* sp. [5, 1 bivalved]; *Gyropleura* sp. [4]; *?Tellinella* sp. [1, bivalved]; '*Quenstedtiidae*', gen. nov. [1]; Clavagellidae, gen. nov. [3]. **Gastropods:** *?Umboniinae*, gen. nov. [27]; Turritellidae [1]; *?Rhabdoconcha* sp. [2]; Cerithiidae [1]; Strombidae, gen. nov. [3]; Buccinacea sp. [1]; *Lyria* sp. [2]; *?Volutomorpha* sp. [2]; Volutidae, cf. *Melo* [1]; *?Cancellariidae* [1]; *?Neogastropods* indet. [5]. **Cephalopod:** *Cimonia* cf. *sowerbyana* (d'Orbigny) [1]. **Corals:** *Cunnolites* sp. [4].

Collected in scree or from slipped blocks. **Echinoids:** *Orthopsis miliaris* (d'Archiac) [4]; *Salenia nutrix* Peron & Gauthier [1]; *Noetlingaster* sp. [1, fragment]; '*Globator*' *bleicheri* (Thomas & Gauthier) [2]; *Faujasia eccentripora* Lees [6]; *Petalobrissus* sp. [2]; *Hemipneustes compressus* Noetling [1]; *Hemipneustes* sp. [2, fragments]. **Bivalves:** *Cucullaea* sp. A [2, 1 bivalved]; *Neithea regularis* (Schlotheim) [1]; *Pycnodonte vesicularis* (Lamarck) [2]; *?Pycnodonte uncinella* (Leymerie) [2]; *Agerostrea ungulata* (Schlotheim) [3]; *Scabrotrigonia* sp. [14]; *Glabrobournonia arabica* Morris & Skelton, sp. nov. [1]; Radiolitidae [1]; Tancrediidae, cf. *Tatella*, sp. nov. [1, bivalved]. **Gastropods:** '*Tectus*' sp. [1]; Turbinidae [1];

?Umboniinae, gen. nov. [1]; ?Turritellidae indet. [1]; '*Ampullina* aff. *splendida*' (Deshayes) [2]; *Tylostoma incerta* (Forbes) [2]; ?Naticidae sp. [1]; ?*Cimolithium* sp. [1]; ?Aporrhaidae sp. [2]; *Lyria* sp. [3]; *Acteonella* sp. cf. *borneensis* Nuttall & Leong [8]; opisthobranch [1]. **Corals:** *Cunnolites* sp. [66]; *Diploctenium* sp. [1]. **Ammonites:** *Brahmaites (Anabrahmaites) vishnu* (Forbes) [1].

Bed 6. **Echinoids:** *Coenholectypus inflatus* (Cotteau & Gauthier) [8]; '*Globator*' *bleicheri* (Thomas & Gauthier) [1]; *Hemipneustes persicus* Cotteau & Gauthier [2]; *Hemiaster hattaensis* Ali [3].

Rebel Rawdah, Section 2

Bed 4: 60–120 cm above basal conglomerate. **Echinoids:** *Goniopygus arabicus* sp. nov. [1]; *Plistophyma asiaticum* Gauthier [1]; *Echinotiara perebaskinei* Lambert [6]; *Faujasia eccentripora* Lees [14]; *Petalobrissus rawdahensis* sp. nov. [3]. **Bivalve:** *Durania* [1]. **Gastropod:** ?'*Ampullina* aff. *splendida*' (Deshayes) [2]. **Decapod crustacean:** limb segments [4].

Bed 5. **Echinoids:** *Faujasia eccentripora* Lees [2].

Beds 6–8. **Echinoids:** *Salenia nutrix* Peron & Gauthier [10]; *Goniopygus arabicus* sp. nov. [6]; *Codiopsis lehmanni* sp. nov. [1]; *Phymechinus perplexus* sp. nov. [6]; ?*Phymechinus* sp. [1]; *Echinotiara perebaskinei* Lambert [58]; *Coenholectypus inflatus* (Cotteau & Gauthier) [1]; '*Globator*' *bleicheri* (Thomas & Gauthier) [1]; *Faujasia eccentripora* Lees [92]; *Petalobrissus rawdahensis* sp. nov. [4]; *Petalobrissus* cf. *setifensis* (Cotteau) [9]; *Hemipneustes arabicus* Ali [1]. **Bivalve:** ?*Ctenoides* sp. [1]; *Durania* form B [4]. **Coral:** *Cunnolites* sp. [1]. **Decapod crustacean:** limb and claw segments [4].

Bed 10. **Echinoids:** *Goniopygus arabicus* sp. nov. [1]; *Glyphopneustes hattaensis* Ali [2]; *Faujasia eccentripora* Lees [1]; *Petalobrissus* sp. [2]. **Bivalves:** *Durania* cf. *apula* (Parona) [1]. **Gastropod:** Strombacea [1].

Bed 11: *Cucullaea* bed immediately overlying orange-weathering band. **Echinoids:** *Noetlingaster paucituberculatus* (Noetling) [1, fragment].

Bed 11 (middle, *ca.* 1 m above orange-weathering band). **Echinoids:** *Goniopygus arabicus* sp. nov. [1]; *Faujasia eccentripora* Lees [6]; *Petalobrissus* sp. [1]; *Nucleopygus magnus* sp. nov. [4]; *Stigmatopygus pulchellus* sp. nov. [2]; *Hemipneustes arabicus* Ali [4]. **Gastropods:** ?Umboniinae, gen. nov. [1]; *Campanile* sp. [1]; *Pyrazus* sp. [1]; Strombidae, gen. nov. [1]; Volutidae sp. [3].

Bed 11: 2.5 m above base. **Echinoids:** *Echinotiara perebaskinei* Lambert [18]; *Coenholectypus* cf. *baluchistanensis* (Noetling) [1]; *Faujasia eccentripora* Lees [49]; *Petalobrissus* sp. [40]. **Gastropod:** '*Ampullina* aff. *splendida*' *(Deshayes) [1].* **Corals:** *Cunnolites* sp. [3]; massive meandroid colony [1].

Bed 11 (unspecified). **Echinoids:** *Salenia nutrix* Peron & Gauthier [2]; *Glyphopneustes emiratensis* Ali [5]; *Hattopsis sphericus* Ali [2]; *Noetlingaster paucituberculatus* (Noetling) [4]; *Phymechinus?* perplexus sp. nov. [1]; *Echinotiara perebaskinei* Lambert [3]; *Coenholectypus* cf. *baluchistanensis* (Noetling) [8]; '*Globator*' *bleicheri* (Thomas & Gauthier) [10]; *Faujasia eccentripora* Lees [46]; *Zuffardia morgani* (Cotteau & Gauthier) [41]; *Petalobrissus rawdahensis* sp. nov. [247]; *Petalobrissus* cf. *setifensis* (Cotteau) [124]. **Bivalves:** '*Modiolus*' aff. *typicus* Forbes [1, bivalved]; *Cucullaea* sp. A [8, bivalved]; *Pholadomya* sp. C. cf. *P. connectans* Forbes [22, bivalved]. **Coral:** *Cunnolites* sp. [1].

Bed 13. **Echinoids:** *Salenia nutrix* Peron & Gauthier [2]; *Glyphopneustes hattaensis* Ali [1]; '*Globator*' *bleicheri* (Thomas & Gauthier) [1]; *Petalobrissus rawdahensis* sp. nov. [230]; *Petalobrissus* cf. *setifensis* (Cotteau) [4]; *Nucleopygus magnus* sp. nov. [3]. **Bivalves:** '*Modiolus*' aff. *typicus* Forbes [1, bivalved]; *Dictyoptychus morgani* (Douvillé) [common]; ?*Biradiolites* aff. *baylei* Toucas [1]; ?*Fragum* sp. [1]; ?Clavagellidae indet. [1]. **Gastropods:** ?Umboniinae, gen. nov. [6]; Turritellidae, sp. [1]; ?*Rhabdoconcha* sp. [1]; ?*Cimolithium* sp. [2]; '*Ampullina* aff. *splendida*' (Deshayes)

[4]; Cypraeidae, sp. [1]; cf. ?Columbellidae [2]; ?Neogastropod indet. [1]. **Corals:** *Cunnolites* sp. [15]; *Diploctenium* sp. [2]; *Aspidastraea* sp. [1].

Bed 14. **Echinoids:** *Noetlingaster paucituberculatus* (Noetling) [5 plus fragments]; *Phymechinus* ? sp. [1]; '*Globator*' *bleicheri* (Thomas & Gauthier) [7]; *Conulus douvillei* (Cotteau & Gauthier) [1]; *Faujasia eccentripora* Lees [7]; *Pygurostoma morgani* Cotteau & Gauthier [3]; *Arnaudaster cylindriformis* sp. nov. [4]; *Petalobrissus rawdahensis* sp. nov. [17]; *Petalobrissus* cf. *setifensis* (Cotteau) [15]; *Petalobrissus linguiformis* (Peron & Gauthier) [4]; ?*Stigmatopygus pulchellus* sp. nov. [6]; *Hemipneustes arabicus* Ali [1]; *H. compressus* Noetling [2]. **Gastropods:** *Campanile* sp. [2]; ?*Campanile* sp. [1]; '*Ampullina* aff. *splendida*' (Deshayes) [2]; ?*Pseudocassis* sp. [1]; Strombidae, gen. nov. [2]; Fasciculariidae, sp. [1]; ?Volutidae indet. [1]. **Corals:** *Aspidastraea* sp. [1].

Bed 15. **Echinoids:** *Conulus douvillei* (Cotteau & Gauthier) [2]; *Petalobrissus rawdahensis* sp. nov. [25]; *Hemipneustes compressus* Noetling [2]. **Bivalves:** ?*Granocardium* sp. [3]; rudist [1]. **Gastropods:** *Pyrazus* sp. [2]; Cerithiidae [1]; ?Naticidae, sp. [1]; Strombidae gen. nov. [3]. **Corals:** *Cunnolites* sp. [21]; *Aspidastraea* sp. [9]; massive meandroid colony [1].

Beds 16–19. **Bivalve:** '*Modiolus*' aff. *typicus* Forbes [1, bivalved]. **Corals:** *Cunnolites* sp. [2]; *Aspidastraea* sp. [2].

Bed 16. **Echinoids:** '*Globator*' *bleicherei* (Thomas & Gauthier) [3]; *Faujasia eccentripora* Lees [3]; *Petalobrissus rawdahensis* sp. nov. [5]. **Bivalves:** *Neithea regularis* (Schlotheim) [1] *Durania* spp. [several]; Veneridae [2]. **Gastropods:** ?*Rhabdoconcha* sp. [1]; ?Cerithiidae [1]; '*Ampullina*' aff. *splendida* (Deshayes) [3]; Strombidae [1]; Cypraeidae [1].

Bed 18. **Echinoid:** *Pygurostoma morgani* Cotteau & Gauthier [1]. Bivalves: ?*Granocardium* sp. [1]. **Gastropods:** ?Umboniinae gen. nov. [1]; ?*Cimolithium* sp. [2]; Strombidae, gen. nov. [1].

Bed 19. **Echinoids:** *Noetlingaster paucituberculatus* (Noetling) [4]; *Coenholectypus inflatus* (Cotteau & Gauthier) [1]; '*Globator*' *bleicheri* (Thomas & Gauthier) [8]; *Vologesia rawdahensis* Ali [1]; *Zuffardia morgani* (Cotteau & Gauthier) [5]; *Faujasia eccentripora* Lees [19]; *Arnaudaster cylindriformis* sp. nov. [1]; *Petalobrissus rawdahensis* sp. nov. [73]; *Petalobrissus* cf. *setifensis* (Cotteau) [23]; *Petalobrissus linguiformis* (Peron & Gauthier) [5]; ?*Stigmatopygus pulchellus* sp. nov. [1]; *Pygurostoma morgani* Cotteau & Gauthier [2]; *Hemipneustes compressus* Noetling [1]; *Hemipneustes persicus* (Cotteau & Gauthier) [1]. **Bivalves:** ?*Granocardium* sp. [2]; *Isognomon* sp. [1]; ?Lucinidae indet. [1]; *Dictyoptychus morgani* (Douvillé) [1]; Veneridae, gen. indet. [1]. **Gastropods:** ?Umboniinae, gen. nov. [9]; ?*Rhabdoconcha* sp. [1]; ?Cerithiidae [5]; *Campanile* sp. [4]; '*Ampullina* aff. *splendida*' (Deshayes) [3]; *Tylostoma incerta* (Forbes) [2]; ?Naticidae [4]; Strombidae, gen. nov. [5]; Cypraeidae, sp. [1]; Fasciolariidae or Buccinidae [1]; *Canalicella* sp. [1]; Volutidae [3]; *Acteonella* sp. [1]. **Corals:** *Neocaeniopsis reussi* (Edwards & Haime) [1]; *Astrogyra edwardsi* (Reuss) [1]; cerioid colonies [2]; *Cunnolites* sp. [17]; *Diploctenium* sp. [1]; *Aspidastraea* sp. [8]; massive meandrine colonies [5].

Bed 20. **Echinoids:** '*Globator*' *bleicheri* (Thomas & Gauthier) [2]; *Faujasia eccentripora* Lees [2]; *Petalobrissus linguiformis* (Peron & Gauthier) [1]; *Petalobrissus* sp. [1]; *Hemipneustes compressus* Noetling [1]; *Hemipneustes persicus* (Cotteau & Gauthier) [1]. **Gastropods:** ?*Angaria* sp. [1]; ?Umboniinae gen. nov. [2]; '*Ampullina* aff. *splendida*' (Deshayes) [3]; Strombidae, gen. nov. [5].

Bed 21 (base). **Echinoids:** *Noetlingaster paucituberculatus* (Noetling) [1]; '*Globator*' *bleicheri* (Thomas & Gauthier) [1]; *Conulus douvillei* (Cotteau & Gauthier) [2]; *Faujasia eccentripora* Lees [22]; *Zuffardia morgani* (Cotteau & Gauthier) [5]; *Pygurostoma morgani* Cotteau & Gauthier [7]; *Arnaudaster cylindriformis* sp. nov. [1]; *Petalobrissus rawdahensis* sp. nov. [45]; *Petalobrissus* cf. *setifensis* (Cotteau) [44]; *Petalobrissus linguiformis* (Peron & Gauthier) [4]; ?*Stigmatopygus pulchellus* sp. nov. [7]; *Hemip*

neustes compressus Noetling [16]; *Hemipneustes persicus* (Cotteau & Gauthier) [22]. **Bivalves:** *Barbatia* cf. *morgani* (Douvillé) [3, bivalved]; *Pycnodonte vesicularis* (Lamarck) [1]; heterodont indet. [1]. **Gastropods:** *Campanile* sp. [1]; *'Ampullina* aff. *splendida'* (Deshayes) [1]; Naticidae [2]; *Tylostoma incerta* (Forbes) [1]; Strombidae, gen. nov. [1]; ?Fasciolariidae [1]; bullaeform opisthobranch [1]. **Ammonite:** *Desmophyllites diphylloides* (Forbes) [1].

Bed 21 (middle). **Gastropods:** *'Ampullina* aff. *splendida'* (Deshayes) [4]; Strombidae, gen. nov. [3]; Strombidae, sp. [1]; ?*Hercorhynchus* sp. [1]; ?Buccinacea, sp. [1]; neogastropod, gen. A [2]; neogastropod, gen. B [1].

Bed 22. **Echinoids:** *'Globator' bleicheri* (Thomas & Gauthier) [1]; *Faujasia eccentripora* Lees [3]; *Petalobrissus rawdahensis* sp. nov. [13]; *Hemipneustes compressus* Noetling [1]. **Gastropods:** *'Ampullina* aff. *splendida'* (Deshayes) [2]; ?Buccinacea [1].

Bed 23 (base). **Echinoids:** *Petalobrissus* sp. [1]. **Gastropods:** *Pyrazus* sp. [1]; Naticidae [1].

Beds 23–25. **Echinoids:** *Petalobrissus* sp. [5]; *Faujasia eccentripora* Lees [1]. **Bivalves:** ?*Biradiolites* aff. *baylei* Toucas [2].

Bed 25. **Echinoids:** *Noetlingaster paucituberculatus* (Noetling) [4]; *Faujasia eccentripora* Lees [3]; *Zuffardia morgani* (Cotteau & Gauthier) [1]; *Petalobrissus* sp. [11]. **Bivalve:** ?Lucinidae indet. [1].

Bed 26. **Echinoids:** *Coenholectypus inflatus* (Cotteau & Gauthier) [1]; *Arnaudaster cylindriformis* sp. nov. [1]; *Pygurostoma morgani* Cotteau & Gauthier [2]; *Petalobrissus rawdahensis* sp. nov. [5]; *Petalobrissus* cf. *setifensis* (Cotteau) [3]; *Hemipneustes compressus* Noetling [2]; *Hemipneustes* sp. fragment [1]. **Bivalve:** *Neithea* sp. [1].

Bed 27. **Echinoids:** *Hemipneustes compressus* Noetling [2].

Bed 28. **Bivalves:** Indet. small rudists.

Loose: a little below beds 21/22 and probably derived from them. **Echinoids:** *Hemipneustes arabicus* Ali [1].

Loose: scree from level of bed 11 (derived from beds 13–15 mostly). **Echinoids:** *Coenholectypus inflatus* (Cotteau & Gauthier) [1]; *Conulus douvillei* (Cotteau & Gauthier) [1]; *Faujasia eccentripora* Lees [14]; *Zuffardia morgani* (Cotteau & Gauthier) [3]; *Petalobrissus linguiformis* (Peron & Gauthier) [6]; *Petalobrissus* sp. [2].

Loose, scree. Echinoids: *Glyphopneustes hattaensis* Ali [2]; *Echinotiara perebaskinei* Lambert [2]; *Coenholectypus inflatus* (Cotteau & Gauthier) [1]; *'Globator' bleicheri* (Thomas & Gauthier) [4]; *Faujasia eccentripora* Lees [32]; *Zuffardia morgani* (Cotteau & Gauthier) [11]; *Arnaudaster cylindriformis* sp. nov. [1]; *Pygurostoma morgani* Cotteau & Gauthier [1]; *Petalobrissus* sp. [62]; *Nucleopygus magnus* sp. nov. [3]; *Hemipneustes persicus* (Cotteau & Gauthier) [4]; *Hemiaster hattaensis* Ali [1]. **Bivalves:** *'Modiolus'* aff. *typicus* Forbes [1, bivalved]; *Spondylus* sp. C [1]; *Amphidonte pyrenaicum* (Leymerie) [1]; *Dictyoptychus morgani* (Douvillé) [1]; *Radiolites* sp. [1]; ?*Biradiolites* aff. *baylei* Toucas [2]. **Gastropods:** ?Umboniinae, gen. nov. [3]; *Pyrazus* sp. [1]; *Campanile* sp. [1]; *'Ampullina* aff. *splendida'* (Deshayes) [1]; ?*Perrisoptera* sp. [1]; *Caricella* sp. [2]; *Acteonella* sp. [1]; *Acteonella* cf. *caucasica* Zekeli [1]. **Corals:** *Cunnolites* sp. [12]; *Aspidastraea* sp. [1].

Loose, lower part of section (from beds 1–11). Echinoids: *Salenia nutrix* Peron & Gauthier [3]; *Goniopygus arabicus* sp. nov. [4]; *Glyphopneustes hattaensis* Ali [4]; *Hattopsis sphericus* Ali [1]; *Noetlingaster paucituberculatus* Noetling [1]; *Phymechinus? perplexus* sp. nov. [4]; *Echinotiara perebaskinei* Lambert [15]; *Coenholectypus baluchistanensis* Noetling [5]; *'Globator' bleicheri* (Thomas & Gauthier) [9]; *Faujasia eccentripora* Lees [80]; *Zuffardia morgani* (Cotteau & Gauthier) [29]; *Petalobrissus* spp. [136]. **Asteroid:** marginal [1]. **Brachiopod:** terebatulid, gen. nov. [1].

Loose, mid-section. Echinoids: *Salenia* sp. [1]; *Zuffardia morgani* (Cotteau & Gauthier) [6]; ?*Stigmatopygus pulchellus* sp. nov. [1]. **Corals:** *Cunnolites* sp. [2]; *Aspidastraea* sp. [1].

Jebel Rawdah, Section 3a

Bed 2. Echinoids: *Goniopygus arabicus* sp. nov. [2]. **Bivalve:** *Durania* sp. [1]. **Gastropod:** *Acteonella* sp. [1].

Bed 4. Echinoid: *Echinotiara perebaskinei* Lambert [1]. **Bivalves:** *Pycnodonte vesicularis* (Lamarck) [1]; *Amphidonte pyrenaicum* (Leymerie) [2, bivalved].

Bed 5. Bivalves: *'Modiolus'* aff. *typicus* Forbes [1, bivalved]; ?*'Mytilus' nitens* Forbes [1, bivalved]; *Barbatia* sp. B [3]; *Neithea regularis* (Schlotheim) [3]; *Amphidonte pyrenaicum* (Leymerie) [3]; *Agerostrea ungulata* (Schlotheim) [9]; Eligmidae [5, bivalved]; *Crassitellites* sp. [5].

Bed 7 (near top). Echinoid: *'Globator' bleicheri* (Thomas & Gauthier) [1]. **Bivalves:** *Pycnodonte vesicularis* (Lamarck) [1]; *Agerostrea ungulata* (Schlotheim) [1, bivalved]; ?*Clavagella* sp. [tubes]. **Gastropods:** Naticidae, indet. [2].

Loose, derived from lower beds. Bivalves: *Plicatula hirsuta* Coquand [1]; ?*Pycnodonte uncinella* (Leymerie) [2, bivalved]. **Gastropod:** Turritellidae [1].

Jebel Rawdah, Section 3b

Bed 2 (lower part). Echinoids: *Orthopsis miliaris* (d'Archiac) [1]; *Glyphopneustes hattaensis* Ali [1]; *Circopeltis emiratus* sp. nov. [1]; *Faujasia eccentripora* Lees [3]. **Coral:** *Cunnolites* sp. [1]. **Decapod crustacean:** *Callianassa* (limb segment) [1].

Bed 2 (upper part). Echinoids: *Salenia nutrix* Peron & Gauthier [1]; *Glyphopneustes hattaensis* Ali [1]; *'Globator' bleicheri* (Thomas & Gauthier) [11]; *Petalobrissus rawdahensis* sp. nov [19]; *Petalobrissus* cf. *setifensis* (Cotteau) [4]; *Nucleopygus magnus* sp. nov. [3]. **Coral:** ?*Diploctenium* sp. [1].

Bed 3. Echinoid: *Echinotiara perebaskinei* Lambert [1]. **Bivalve:** *Pycnodonte vesicularis* (Lamarck) [1].

Bed 4. Corals: large meandrine colonies [2]; placoid colony [1].

Bed 5. Echinoids: *Heterodiadema buhaysensis* sp. nov. [1]; *Glyphopneustes hattaensis* Ali [1]; *Coenholectypus inflatus* (Cotteau & Gauthier) [3]; *'Globator' bleicheri* (Thomas & Gauthier) [1]; *Hemipneustes* sp. [1]; *Hemiaster hattaensis* Ali [1]. **Bivalve:** *Pycnodonte vesicularis* (Lamarck) [1].

Bed 5/6. Echinoids: *'Globator' bleicheri* (Thomas & Gauthier) [8]; *Hemipneustes persicus* Cotteau & Gauthier [1]; *Mecaster victoris* Lambert [47].

Bed 6. Echinoid: *Circopeltis emiratus* sp. nov. [1]. **Bivalve:** Eligmidae [1]. **Gastropod:** *Tylostoma incerta* (Forbes) [1].

Bed 7. Echinoids: *Coenholectypus inflatus* (Cotteau & Gauthier) [1]; *Hemipneustes persicus* Cotteau & Gauthier [1]. **Bivalves:** *Barbatia* sp. B [1, bivalved]; *'Modiolus'* aff. *typicus* Forbes [2, bivalved].

Bed 8. Echinoids: *Orthopsis miliaris* (d'Archiac) [1]; *Actinophyma spectabile* Cotteau & Gauthier [1]; *Coenholectypus* sp. [1]; *Vologesia rawdahensis* Ali [1]; *Faujasia eccentripora* Lees [1]; *Mecaster* sp. [6]. **Coral:** *Cunnolites* sp. [1]. **Decapod crustacean:** pincer [1].

Bed 9. Echinoids: *Orthopsis miliaris* (d'Archiac) [7]; *Noetlingaster* sp. [1, fragment]; *Actinophyma spectabile* Cotteau & Gauthier [1]; *'Globator' bleicheri* (Thomas & Gauthier) [1]; *Faujasia eccentripora* Lees [3]; *Hemipneustes compressus* Noetling [2]; *Hemiaster* sp. cf. *H. hattaensis* Ali [1]; *Mecaster victoris* Lambert [1]; *Proraster geayi* Cottreau [2]. **Bivalves:** *Cucullaea* sp. A [4]; *Scabrotrigonia* sp. [8, 1 bivalved]; ?Tancrediidae, sp. nov. [1]. **Gastropods:** *Acteonella* sp. cf. *borneensis* Nuttall & Leong [1]; *Acteonella sp.* [2]. **Corals:** *Cunnolites* sp. [8]; *Diploctenium* sp. [1]; thamnasteroid colony [1].

Bed 11. Echinoids: *Coenholectypus inflatus* (Cotteau & Gauthier) [1]; *'Globator' bleicheri* (Thomas & Gauthier) [1]; *Arnaudaster cylindriformis* sp. nov. [1]. **Bivalves:** *Barbatia* sp. B [2]; *'Modiolus'* aff. *typicus* Forbes [1, bivalved]; ?*Pycnodonte uncinella* (Leymerie) [3, bivalved]; *Amphidonte pyrenaicum* (Leymerie) [2, 1 bivalved];

Agerostrea ungulata (Schlotheim) [21]; *Scabrotrigonia* sp. [7, 1 bivalved]. **Gastropod:** *Caricella* sp. [1].

Loose. **Echinoids:** *Prionocidaris morgani* (Gauthier) [1]; *Orthopsis miliaris* (d'Archiac) [3]; *Coenholectypus inflatus* (Cotteau & Gauthier) [6]; *'Globator' bleicheri* (Thomas & Gauthier) [3]; *Conulus douvillei* (Cotteau & Gauthier) [4]; *Hemipneustes compressus* Noetling [1].

Loose near top of section. **Echinoids:** *Arnaudaster cylindriformis* sp. nov. [1]; *?Linthia sudanensis* (Bather) [1].

Jebel Rawdah, Section 4

Bed 1. **Bivalves:** *Dictyoptychus morgani* (Douvillé) [1]; *Praeradiolites* cf. *subtoucasi* Toucas [4]; *Pseudosabinia* aff. *klinghardti* Boehm [3]; *Pseudosabinia* sp. [1].

Bed 1/2. **Echinoids:** *Phymosoma hexoaporum* Lambert [1]; *'Globator' bleicheri* (Thomas & Gauthier) [6]. **Bivalves:** *Scabrotrigonia* sp. [2]; *Glabrobournonia arabica* Morris & Skelton, sp. nov. [21].

Bed 2 (mostly near top). **Echinoids:** *Echinotiara perebaskinei* Lambert [1]; *Coenholectypus* sp. indet. [1]; *'Globator' bleicheri* (Thomas & Gauthier) [3]; *Faujasia eccentripora* Lees [1]; *Zuffardia morgani* (Cotteau & Gauthier) [2]; *Petalobrissus* cf. *setifensis* (Peron & Gauthier) [1]; *Hemiaster hattaensis* Ali [1]. **Bivalves:** *Neithea regularis* (Schlotheim) [1]; *Pycnodonte vesicularis* (Lamarck) [1]; *?Pycnodonte uncinella* (Leymerie) [3, 1 bivalved]; *Amphidonte pyrenaicum* (Leymerie) [1]; *Scabrotrigonia* sp. [1]. **Gastropod:** *Acteonella* sp. cf. *borneensis* Nuttall & Leong [1].

Bed 4. **Echinoids:** *Glyphopneustes hattaensis* Ali [1]; *Circopeltis emiratus* sp. nov. [1]; *'Globator' bleicheri* (Thomas & Gauthier) [4]; *Faujasia eccentripora* Lees [2]; *Petalobrissus* sp. [1]. **Corals:** *Cunnolites* sp. [2]; *Aspidastraea* sp. [1].

Bed 5. **Echinoid:** *'Globator' bleicheri* (Thomas & Gauthier) [1].

Bed 8. **Echinoids:** *Orthopsis miliaris* (d'Archiac) [1]; *Echinotiara perebaskinei* Lambert [1]; *'Globator' bleicheri* (Thomas & Gauthier) [3]; *Conulus douvillei* (Cotteau & Gauthier) [1]; *Petalobrissus* cf. *setifensis* (Cotteau) [3].

Bed 9. **Bivalves:** *Amphidonte pyrenaicum* (Leymerie) [1]; *Scabrotrigonia* sp. [common].

Bed 10. **Echinoids:** *Orthopsis miliaris* (d'Archiac) [6]; *Salenia nutrix* Peron & Gauthier [1]; *'Globator' bleicheri* (Thomas & Gauthier) [10]. **Bivalve:** *Dictyoptychus* sp. [1]. **Corals:** cerioid colony [1]; placoid colony [1].

Bed 12. **Echinoids:** *Coenholectypus* sp. [1]; *'Globator' bleicheri* (Thomas & Gauthier) [5]; *Nucleopygus magnus* sp. nov. [1]. **Sponge:** chaetetid [1].

Bed 13. **Echinoids:** *Noetlingaster emiratescus* Ali [2]; *Coenholectypus inflatus* (Cotteau & Gauthier) [1]; *'Globator' bleicheri* (Thomas & Gauthier) [3]; *Conulus douvillei* (Cotteau & Gauthier) [1]; *Hemiaster hattaensis* Ali [1].

Bed 15. **Echinoids:** *Orthopsis miliaris* (d'Archiac) [1]; *'Globator' beleicheri* (Thomas & Gauthier) [1]. **Coral:** *Actinacis* sp. [1].

Bed 18. **Echinoid:** *Coenholectypus* sp. [1].

Bed 19. **Echinoids:** *Coenholectypus inflatus* (Cotteau & Gauthier) [1]; *'Globator' bleicheri* (Thomas & Gauthier) [1]; *Pygurostoma morgani* Cotteau & Gauthier [1].

Bed 22/23. **Echinoids:** *Coenholectypus inflatus* (Cotteau & Gauthier) [1]; *Faujasia eccentripora* Lees [1].

30 cm below top of measured section. **Echinoids:** *Coenholectypus inflatus* (Cotteau & Gauthier) [1]. **Bivalve:** *Neithea regularis* (Schlotheim) [1].

Loose, a little below the top of the section. **Echinoids:** *Hemipneustes arabicus* Ali [1].

Loose at level of bed 3. **Echinoid:** *Petalobrissus linguiformis* (Peron & Gauthier) [1].

Loose. **Echinoids:** *Orthopsis miliaris* (d'Archiac) [1]; *Conulus douvillei* (Cotteau & Gauthier) [1]; *Petalobrissus* sp. [1]. **Bivalves:** *Amphidonte pyrenaicum* (Leymerie) [2].

Jebel Faiyah, Section 1a

Bed 6. **Bivalves:** *Hippurites* aff. *lapeirousei* Goldfuss [1 colony].

Bed 8. **Bivalves:** *Agerostrea ungulata* (Schlotheim) [2]; *?Pycnodonte uncinella* (Leymerie) [18]; *?Amphidonte* cf. *pyrenaicum* (Leymerie) [1].

Jebel Faiyah, Section 1b

Bed 2 (lower part). **Echinoids:** *Hattopsis paucituberculatus* sp. nov. [6]. **Corals:** *Polytremacis* sp. [1]; *Astraraea* sp. [1]; *Hydnophoraraea* sp. [1]. **Sponge:** chaetetid [1].

Bed 2 (upper part). **Echinoids:** cidarid [1]; *Orthopsis miliaris* (d'Archiac) [1]; *Salenia nutrix* Peron & Gauthier [2]; *Glyphopneustes hattaensis* Ali [1]; *Hattopsis paucituberculatus* sp. nov. [1]; *'Globator' bleicheri* (Thomas & Gauthier) [1]; *Nucleopygus magnus* sp. nov. [1]; *Hemiaster* sp. cf. *H. hattaensis* Ali [1]. **Bivalves:** *Hippurites* cf. *lapeirousei* Goldfuss [1 colony]; *Hippurites* aff. *cornucopiae* Defrance [1]; *Dictyoptychus morgani* (Douvillé) [2]; *Biradiolites* aff. *baylei* Toucas [1]; *Durania* cf. *gaensis* (Dacqué) [1]. **Decapod crustacean:** pincers [2].

Bed 4. **Bivalves:** *Hippurites* aff. *lapeirousei* Goldfuss [2]. **Corals:** *Polytremacis* sp. [1]; *Hydnophoraraea* sp. [1]; *Paraplacocoenia orbignyana* (Reuss) [1]; *Moltkia isis* Sreenstrup [1].

Bed 5. **Echinoid:** *Glyphopneustes hattaensis* Ali [2].

Bed 6. **Echinoid:** cidarid spine [1]. **Coral:** *Moltkia isis* Sreenstrup [1].

Bed 7. **Echinoids:** cidarid spine [1]; *Mimiosalenia quinquetuberculata* sp. nov. [21]; *Hattopsis sphericus* Ali [1]; *'Globator' bleicheri* (Thomas & Gauthier) [36].

Bed 8. Coral: *Cunnolites* sp. [1].

Loose (derived from beds 2–5). **Echinoids:** *Hattopsis paucituberculatus* sp. nov. [5]. **Bivalves:** *Spondylus* sp. C [2]. **Nautiloid:** *Deltoidonautilus salisfilius* sp. nov. [1]. **Corals:** *Polytremacis* sp. [5]; *Cunnolites* sp. [1]; *Paraplacocoenia orbignyana* (Reuss) [1]; *Hydnophoraraea* sp. [5]; turbinate solitary [1]; cerioid colonies (6 genera) [14]; flabellate solitary [1]; phaceloid colony [1]. **Branching algae** [1]. **Sponge:** chaetetid [1]. **Decapod crustacean:** crab carapace [1].

Jebel Faiyah – southern nose of Jebel (bed numbers as in section 1a)

Bed 8. **Echinoids:** *Salenia* sp. [1]; *Glyphopneustes hattaensis* Ali [8]; *Hattopsis sphericus* Ali [8]; *'Globator' bleicheri* (Thomas & Gauthier) [2]; *Pygurostoma morgani* Cotteau & Gauthier [1]. **Corals:** *Cunnolites* sp. [2].

Loose. **Echinoids:** *Hattopsis sphericus* Ali [1]. **Bivalves:** *?Barbatia* sp. A. cf. *B. morgani* (Douvillé) [1, bivalved]; *Neithea regularis* (Schlotheim) [7]; *?Pycnodonte uncinella* (Leymerie) [18]; *?Plagioptychus* sp. [1]; *Glabrobournonia arabica* Morris & Skelton, sp. nov. [1]; *Hippurites ?cornucopiae* Defrance [11]; *Dictyoptychus morgani* (Douvillé) [3]. **Gastropod:** *Tylostoma incerta* (Forbes) [1]. **Corals:** *Moltkia isis* Streenstrup [1]; *Cunnolites* sp. [3]; *Hydnophoraraea* sp. [2]; *Paraplacocoenia orbignyana* (Reuss) [1]; cerioid colonies (3 genera) [4]; phlacoid colony [1]; thamnasteroid colony [1].

Jebel Faiyah, Section 2

Basal 1 m shell bed. **Bivalves:** *Glabrobournonia arabica* Morris & Skelton, sp. nov. [3]. **Nautiloids:** *Cimonia* cf. *sowerbyana* (d'Orbigny) [1]; *Deltoidonautilus salisfilius* sp. nov. [2].

Jebel Bu Milh, Section 1

Bed 1. **Bivalves:** *Pseudosabinia* aff. *klinghardti* (Boehm) [4]; *Durania* cf. *gaensis* (Dacqué).

Bed 3. **Bivalves:** *'Modiolus'* aff. *typicus* Forbes [1, bivalved]; *Lyrio-*

chlamys ternatus (Münster) [2]; *Neithea regularis* (Schlotheim) [1]; *?Plagioptychus* sp. [4, lids]; *Dictyoptychus morgani* (Douvillé) [1, juvenile]; *Radiolites* sp. [3]; *Eodictyoptychus* aff. *arumaensis* Skelton & El-Asa'ad [2]. **Gastropods:** *?'Angaria'/Liotia* sp. [1, fragment]; *?trochid* [1]; *Discotectus* sp. [26]; *Strigosella* sp. cf. *striolata* (Stolizcka) [2]; *Euchelus ornatus* Stolizcka [3]; *?Umbonium greyi* Lees [1]; *'Turritella'* sp. [1]; *'Turritella'* sp. 1 ?= *Nairiella multistriata* (Reuss) [4]; *Vermetus* sp. [2]; *Campanile curtum* Douvillé [1]; *Campanile persicum* Douvillé [2]; *Campanile* aff. *breve* Lees [1, fragment]; *Campanile morgani* Douvillé [1]; *Campanile* sp. [6, internal moulds]; *Campanile* cf. *ganesha* Noetling [4]; *Cimolithium* sp. nov. [2]; *Pyrazus* sp. [1]; *Paryphostoma morgani* Douvillé [1]; *Pugnellus* sp. [2]; *Ampullina* aff. *splendida* (Deshayes) [30+]; *'Euspira' lirata* J. de C. Sowerby [22]; *'Natica' pagoda* Forbes [2]; *Tylostoma incerta* (Forbes) [5]; *Confusiscala* sp. [1]; *'Cypraea' kayeii* Forbes [2]; *Hipponyx* sp. [1]; *'Fulguraria' multistriata* Stolizcka [1]; fasciolariid [1]; ?Rapanidae gen. indet. [1]; *'Murex'* sp. [1]; *'Trophon' oldhamianum* Stolizcka [1]; *Volutoderma elongata* Stolizcka [1]; *Volutolithes latisepta* Stolizcka [2]; *Caricella pyriformis* Forbes [2]; *Caricella* sp. [2]; *'Voluta'* sp. or spp. [3]; *Trochactaeon* sp. [1]; *Acteonella* cf. *caucasica* Zekeli [30+]; *Acteonella caucasica* Zekeli subsp. *grossouvrei* Cossmann [10]; *Acteonella laevis laevis* (J. de C. Sowerby) [4]; *Acteonella elongata* Kollmann [4]. **Corals:** *Aspidastraea* sp. [1]; *Hydnophoraraea* sp. [2].

Jebel Bu Milh, Section 2

Bed 4. Gastropods: *Acteonella* cf. *caucasica* Zekeli [74]; *Acteonella elongata* Kollmann [1]; *Acteonella laevis* (J. de C. Sowerby) [3]; *Acteonella* cf. *laevis zekelii* Kollmann [1]. **Bivalves:** *Lapeirousia* sp. [2].

Beds 7/8. Echinoids: *Petalobrissus* cf. *setifensis* (Cotteau) [1]. **Bivalves:** *Barbatia* sp. B [12, 4 bivalved]; *Cucullaea* sp. A [2, bivalved]; *Glycymeris* sp. [1]; *'Platyceramus'* sp. [1]; *Lyriochlamys ternatus* (Münster) [1]; *Neithea regularis* (Schlotheim) [1]; *Spondylus* sp. [4, bivalved]; *Plicatula hirsuta* Coquand [5]; *Plagiostoma* sp. [2]; *Crassatellites* sp. [5]; *Eodictyoptychus* aff. *arumaensis* Skelton & El-Asa'ad [1]; *Biradiolites* aff. *baylei* Toucas [1]. **Gastropods:** *Calliomphalus* sp. [2]; *?Calliomphalus* or *Helicanthus* sp. [1]; *?'Angaria'* sp. [2]; Cyclostrematid/Liotid gen. nov. [1]; cf. *'Turbo' punctatus* Zekeli [1, fragment]; *Discotectus* sp. 1 [common]; *Discotectus* sp. 2 [common]; *Strigosella* sp. cf. *striolata* (Stolizcka) [common]; *Nerita* spp. [occurs]; *'Lissocheilus' persicus* (Douvillé) [4]; *'Turritella'* sp. 1 ?= *Nairiella multistriata* (Reuss) [7]; *'Turritella'* sp. cf. *morgani* Douvillé [1]; *'Turritella'* sp. 3 (?= *Roemeriella nerinea* Akopyan (*non* Römer)) [2]; *Campanile ?robustum* Dou-

villé [1]; *Campanile curtum* Douvillé [26]; *Campanile ?persicum* Douvillé [2]; *Campanile* aff. *breve* (Lees) [5]; *Campanile morgani* Douvillé [1]; *Cimolithium* sp. nov. [72]; *Semivertagus* cf. *arcotense* Stolizcka [1]; cf. *Pyrazella (Plicopyrazus)* [1]; *Pyrazus pyramidatus* Douvillé [1]; *Exechocirsus* sp. 1 [2]; *Exechocirsus* sp. 2 [1]; *?Exechocirsus* sp. [2]; *?Semivertagus* sp. cf. *arcotense* (Stolizka) [7]; *Hantkenia louristana* Douvillé [5]; Strombidae gen. nov. *giganteus* Noetling [6]; Strombidae gen. nov. *digitatus* Noetling [2]; *'Helicaulax'* sp. [4]; *Ampullina* aff. *splendida* (Deshayes) [100]; *'Euspira lirata'* (J. de C. Sowerby) [1]; *?Tylostoma incerta* (Forbes) [12]; *'Confusiscala'* sp. cf. *turbinata* Forbes [5]; *'Calyptraea' elevata* Forbes [1]; *Thlacodes lamellosus* Stolizcka [1]; *Lathyrus* sp. [1]; *Lathyrus* sp. cf. *'Ornopsis' digressa* (Wade) [1]; *?Bellifusus* sp. [1]; *?Pseudoliva* sp. [2]; *'Voluta' citharina* Forbes [1]; *Volutoderma* sp. [2]; *Caricella pyriformis* Forbes [20+]; *'Voluta'* sp. [11]; *'Voluta'* sp. [21]; *Voluta cameleo* Forbes [1]; *Volutoderma* sp. [1]; *Lyria crassicostata* Dujardin [2]; *?Naronia eximia* Stolizcka [1]; *Acteonella caucasica* Zekeli *grossouvrei* Cossmann [46]; *Acteonella caucasica caucasica* Zekeli [31]; *Acteonella caucasica* Zekeli subsp. nov. [1]; *Acteonella laevis laevis* (J. de C. Sowerby) [3]; *?Acteonella laevis* J. de C. Sowerby *zekelii* Kollman [1]; *?Acteonella elongata* Kollman [4]; *Neocylindrites minutus* (Stolizcka) [2]. **Ammonite:** *Nostoceras (Nostoceras) major* Kennedy & Cobban [1]. **Nautiloids:** *Deltoidonautilus salisfilius* sp. nov. [9]. **Corals:** *Cunnolites* sp. [6]; cerioid colonies (2 genera) [3]. **Sponges** [7].

Bed 10. Bivalves: *Vaccinites oppeli* (Douvillé) [abundant, in situ].

Qarn Murrah

Rudist level near top of section. Bivalves: *Osculigera* cf. *vautrinioides* Vögel [32]; *Vaccinites vesiculosus* (Woodward) [13];?*Vaccinites loftusi* (Woodward) [3]; *Glabrobournonia arabica* Morris & Skelton, sp. nov. [16]; *Pseudosabinia* aff. *klinghardti* (Boehm) [1]; *Pseudopolyconites* aff. *parvus* Milovanovic [1]; *Colveraia variabilis* Klinghardt [1]. **Corals:** *Cunnolites* sp. [2]; cerioid colonies (2 genera) [3].

Qarn Mulayh

Lower part. Bivalves: *Pironaea* cf. *polystylus* Pirona [3]; *Durania* form A [2]; *Durania* sp. [1].

7·7 m below the top of the section. Bivalves: *Torreites sanchezi (Douvillé) milovanovici* Grubic [3].

Unspecified level. Bivalves: *Colveraia variablilis* Klinghardt [1].

Late Campanian-Maastrichtian echinoids from the United Arab Emirates-Oman border region

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CONTENTS

SYNOPSIS. Forty-five echinoid species, 14 of them new, are described from the Maastrichtian Simsima Formation exposed along the western margins of the North Oman Mountains. The stratigraphic distribution of over 2,500 individual fossil echinoids has been recorded and used to assess echinoid abundance quantitatively and identify recurrent assemblages of species. Although approximately equal numbers of regular and irregular echinoid species are known, irregular echinoids greatly outnumber regulars in abundance. Furthermore, most species are rare, with just five making up more than 67% of the total collection. Regular echinoids are divisible into four ecological groups, ranging from hard-ground dwellers living within active wave-surge environments, to herbivores living in protected subtidal soft-bottom environments. Five ecological groups of irregular echinoid are distinguished, largely on the basis of their inferred feeding strategies. Seven echinoid assemblages are distinguished and their palaeoecological setting interpreted on the basis of the autecology of included species, associated macrofauna and lithofacies evidence. One new genus of Goniopygidae, *Mimiosalenia*, is described and the following new species are erected: *Prionocidaris? emiratus*, *Heterodiadema buhaysensis*, *Salenia microprocta*, *Goniopygus arabicus*, *Mimiosalenia quinquetuberculata*, *Codiopsis lehmannae*, *Hattopsis paucituberculatus*, *Circopeltis? emiratus*, *Phymechinus? perplexus*, *Coptodiscus magniproctus*, *Petalobrissus rawdahensis*, *Nucleopygus magnus*, *Stigmatopygus? pulchellus*, *Arnaudaster cylindriformis*.

INTRODUCTION

Late Cretaceous echinoid faunas, though well-documented in both Europe and America, remain relatively little studied elsewhere in the world. Those of the Middle East are particularly poorly known. Much of our knowledge of Tethyan late Cretaceous echinoid faunas comes from the major monographic works of the last century such as those dealing with Algeria (Cotteau *et al.* 1881), Iran (Cotteau & Gauthier 1895; Gauthier 1902) and Baluchistan (Noetling 1897), all of which are now in great need of revision and updating. Additional major late Cretaceous faunas were described during the early part of this century from Libya (Checchia-Rispoli 1930, 1931a,b, 1932a,b, 1933) and from Madagascar (Cottreau 1908; Lambert 1933).

Until recently the late Cretaceous faunas of the Arabian Peninsula remained virtually unknown. Duncan (1865) described a few Cenomanian echinoids from south eastern Oman, while Lees (1928) described two new late Cretaceous echinoid species from north western Oman. Clegg (1933) described a large number of echinoids from the Persian Gulf, but only two of these were Cretaceous, and neither appears to be late Cretaceous in age.

The first indication of the rich late Cretaceous echinoid fauna of the Arabian Peninsula came with the publication of Kier's (1972) monograph on the Mesozoic and Tertiary echinoids around Riyadh, Saudi Arabia. In this work he described 11 species from the Campanian-Maastrichtian Aruma Formation, six of which were new to science and the remainder representing species already described by Cotteau & Gauthier (1895) and Gauthier (1902) from southern Iran. Subsequently, Ali (1989, 1992a,b) documented 20 echinoids, including seven new species, from the Simsima and Qahlah Formations of the western Oman Mountains. Smith (in Skelton *et al.* 1990) gave some preliminary records of the echinoid fauna from these beds and Roman *et al.* (1989) gave a preliminary report on the Cretaceous echinoids of the Dhofar region, Oman, including four Campanian/Maastrichtian species.
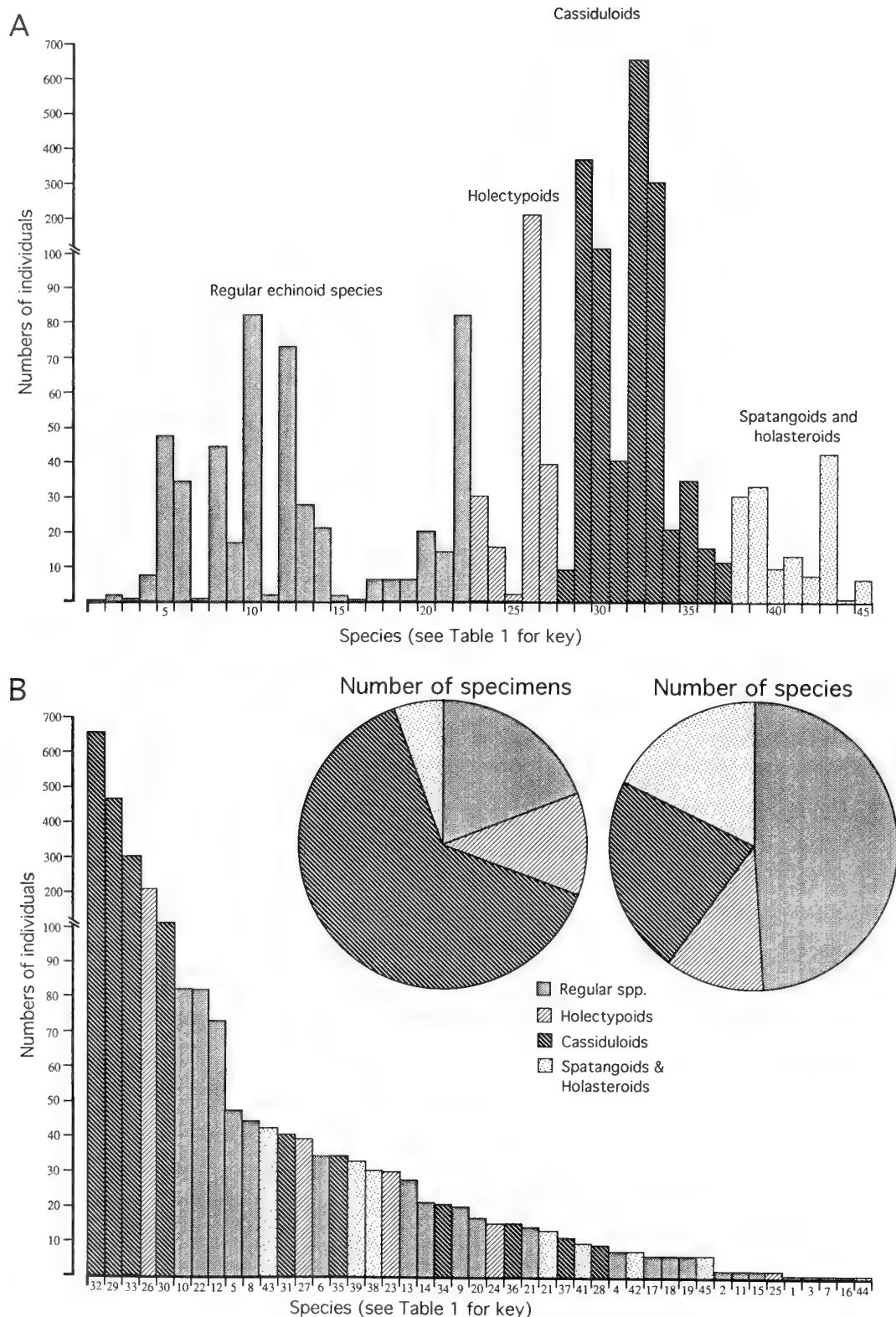
Fig. 1   Relative abundance of species collected from the Maastrichtian Qahlah and Simsima Formations along the United Arab
Emirates-Oman border region (based on *ca.* 2,500 individuals). Species 1–45 are listed in Table 1. Shading distinguishes the four major
taxonomic groups of echinoids. **A**, species arranged systematically. **B**, species arranged in order of specimen abundance. Pie diagrams
represent the number of individuals and number of species for each major taxonomic group.

Table 1. Echinoid species collected from the Qalah and Simsima Formations exposed in the Jebels along the Oman-United Arab Emirates border region.

Class Echinoidea Leske, 1778
  Subclass Cidaroidea Claus, 1880
    Order Cidaroida Claus, 1880
      Family Rhabdocidaridae Lambert, 1900
1.   **Gen. et sp. indet.**

      Family Cidaridae Gray, 1825
        Genus *Prionocidaris* Agassiz, 1863
2.   ***Prionocidaris morgani* (Gauthier, 1902)**
3.   ***Prionocidaris? emiratus* sp. nov.**

  Subclass Euechinoidea Bronn, 1860
    ?Cohort Diadematacea Duncan, 1889
      ?Order Diadematoida Duncan, 1889
        Family Heterodiadematidae Smith & Wright, 1993
          Genus *Heterodiadema* Cotteau, 1864
4.   ***Heterodiadema buhaysensis* sp. nov.**

  Cohort Echinacea Claus, 1876
    Plesion (Order) Orthopsida Mortensen, 1942
      Family Orthopsidae Duncan, 1889
        Genus *Orthopsis* Cotteau, 1864
5.   ***Orthopsis miliaris* (d'Archiac, 1835)**

    Order Calycina Gregory, 1900
      Family Saleniidae Agassiz, 1838
        Genus *Salenia* Gray, 1835
6.   ***Salenia nutrix* Peron & Gauthier, 1881**
7.   ***Salenia microprocta* sp. nov.**

    Order Arbacioida Gregory, 1900
      Family Goniopygidae Smith & Wright, 1993
        Genus *Goniopygus* Agassiz, 1838
8.   ***Goniopygus arabicus* sp. nov.**

        Genus *Mimiosalenia* gen. nov.
9.   ***Mimiosalenia quinquetuberculata* sp. nov.**

      Family Glyphopneustidae Smith & Wright, 1993
        Genus *Glyphopneustes* Pomel, 1883
10.   ***Glyphopneustes hattaensis* Ali, 1992**

      Family Arbaciidae Gray, 1835
        Genus *Codiopsis* Agassiz, 1840
11.   ***Codiopsis lehmannae* sp. nov.**

        Genus *Hattopsis* Ali, 1992
12.   ***Hattopsis sphericus* Ali, 1992**
13.   ***Hattopsis paucituberculatus* sp. nov.**

        Genus *Noetlingaster* Vredenberg, 1911
14.   ***Noetlingaster paucituberculatus* (Noetling, 1897)**
15.   ***Noetlingaster emiratescus* Ali, 1989**
16.   ***Noetlingaster?* sp.**

    Order Phymosomatoida Mortensen, 1904
      Family Phymosomatidae Pomel, 1883
        Genus *Phymosoma* Haime, 1853
17.   ***Phymosoma hexoaporum* Lambert, 1927**

        Genus *Actinophyma* Cotteau & Gauthier, 1895
18.   ***Actinophyma spectabile* Cotteau & Gauthier, 1895**

        Genus *Plistophyma* Peron & Gauthier, 1881
19.   ***Plistophyma asiaticum* Cotteau & Gauthier, 1895**

      Family Stomechinidae Pomel, 1883
        Genus *Circopeltis* Pomel, 1883
20.   ***Circopeltis? emiratus* sp. nov.**

        Genus *Phymechinus* Desor, 1856
21.   ***Phymechinus? perplexus* sp. nov.**

        Genus *Echinotiara* Pomel, 1883
22.   ***Echinotiara perebaskinei* Lambert, 1929**

  Cohort Irregularia Latreille, 1825
    Order Holectypoida Duncan, 1889
      Family Holectypidae Lambert, 1899
        Genus *Coenholectypus* Pomel, 1883
23.   ***Coenholectypus inflatus* (Cotteau & Gauthier, 1895)**
24.   ***Coenholectypus* cf. *baluchistanensis* (Noetling, 1897)**

        Genus *Coptodiscus* Cotteau & Gauthier, 1895
25.   ***Coptodiscus magniproctus* sp. nov.**

      Family Conulidae Lambert, 1911
        Genus '*Globator*' Agassiz, 1840
26.   **'*Globator*' *bleicheri* (Gauthier, 1889)**

        Genus *Conulus* Leske, 1778
27.   ***Conulus douvillei* (Cotteau & Gauthier, 1895)**

    Order Cassiduloida Claus, 1880
      Family Clypeolampadidae Kier, 1962
        Genus *Vologesia* Cotteau & Gauthier, 1895
28.   ***Vologesia rawdahensis* Ali, 1989**

      Family Faujasiidae Lambert, 1905
        Genus *Faujasia* d'Orbigny, 1856
29.   ***Faujasia eccentripora* Lees, 1928**

        Genus *Zuffardia* Checchia-Rispoli, 1917
30.   ***Zuffardia morgani* (Cotteau & Gauthier, 1895)**

      Unnamed family
        Genus *Pygurostoma* Cotteau & Gauthier, 1895
31.   ***Pygurostoma morgani* Cotteau & Gauthier, 1895**

      Family Cassidulidae Agassiz & Desor, 1847
        Genus *Petalobrissus* Lambert, 1916
32.   ***Petalobrissus rawdahensis* sp. nov.**
33.   ***Petalobrissus* cf. *setifensis* (Cotteau, 1866)**
34.   ***Petalobrissus linguiformis* (Peron & Gauthier, 1881)**

        Genus *Stigmatopygus* d'Orbigny, 1856
36.   ***Stigmatopygus? pulchellus* sp. nov.**

        Genus *Nucleopygus* Agassiz, 1840
35.   ***Nucleopygus magnus* sp. nov.**

      Family Echinolampadidae Gray, 1851
        Genus *Arnaudaster* Lambert, 1918
37.   ***Arnaudaster cylindriformis* sp. nov.**

    Order Holasteroida Durham & Melville, 1957
      Family Holasteridae Pictet, 1857
        Genus *Hemipneustes* Agassiz, 1836
38.   ***Hemipneustes compressus* Noetling, 1897**
39.   ***Hemipneustes persicus* Cotteau & Gauthier, 1895**
40.   ***Hemipneustes arabicus* Ali, 1989**

    Order Spatangoida Claus, 1876
      Family Hemiasteridae Clark, 1917
        Genus *Hemiaster* Agassiz, *in* Agassiz & Desor, 1847
41.   ***Hemiaster hattaensis* Ali, 1989**
42.   ***Hemiaster paronai* Checchia-Rispoli, 1921**

        Genus *Mecaster* Pomel, 1883
43.   ***Mecaster victoris* (Lambert, 1932)**

      Family Schizasteridae Lambert, 1905
        Genus *Linthia* Desor, 1853
44.   ***?Linthia sudanensis* (Bather, 1904)**

        Genus *Proraster* Lambert, 1895
45.   ***Proraster geayi* Cottreau, 1908**

Our field collecting in this region has more than doubled the known fauna of late Cretaceous echinoids, making it one of the most diverse assemblages of this age anywhere in the world. Much of the material is well preserved, allowing plating details to be recorded in many species and genera for the first time. Forty four species are recognized (Table 1) and sufficient material has been collected (over 2,500 specimens) to allow a detailed biometric study of most species. Furthermore, bed by bed collecting has enabled me to recognize recurrent assemblages and to place these into their palaeoenvironmental setting, something that has never previously been attempted.

RELATIVE ABUNDANCES OF SPECIES

A total of 2585 specimens were collected and identified to species level, allowing a quantitative assessment of species abundance. This is not entirely accurate in comparison with a previous study of echinoid abundance in the Cenomanian (Smith 1988) where every specimen seen was collected, because the three or four most abundant species are surely undercollected. A few species (e.g. *Petalobrissus rawdahensis* at Jebel Rawdah, section 2, or ‘*Globator*’ *bleicheri* at Jebel Buhays) were so abundant that only a proportion of the observed specimens were eventually collected. There is therefore a bias towards the rarer species. Nevertheless, a number of general conclusions can be drawn from the distributional and abundance data that have been collected.

(a) There are approximately equal numbers of regular and irregular echinoid species (22 regular, 23 irregular) (Fig. 1B). A similar ratio of regular to irregular species is characteristic of the present day biota (Kier 1977) and for extensive collections from the Cenomanian of Great Britain and France (Smith 1988, Neraudeau & Moreau 1989). Amongst the irregular echinoids, cassiduloids (10 species) are more diverse than holectypoids (5 species), spatangoids (5 species) or holasteroids (3 species).

(b) Irregular echinoids greatly exceed regular echinoids in numbers of specimens (Fig. 1B). In total 499 specimens of regular echinoid were collected (19%), and this is likely to overestimate their true relative abundance, since the five most common echinoids were all irregular species and are likely to have been significantly undercollected. This compares well with previous studies, where Smith (1988) found between 10–20% of the total number of echinoid specimens collected (1800 individuals) from the Cenomanian of Wilmington were regular species, and with Neraudeau & Moreau (1989) who reported 22.8% of 5133 individuals collected from the Cenomanian of North Aquitaine were regular species. Therefore regular echinoids achieve a similar species diversity to irregular echinoids, but occur in much lower absolute diversity.

(c) Most species are rare. In terms of numbers of individuals, just five species make up more than 67% of the total collection (Fig. 1A). Four of these five species are cassiduloid, the fifth (8% of the total) is the holectypoid ‘*Globator*’. The most abundant species are cassiduloids and two of the three species of *Petalobrissus* together form more than 36% of the total number of individuals collected. In reality these species are even more dominant, since they were certainly undercollected in comparison to rare species, possibly by as much as a factor of two.

In comparison, the most abundant regular echinoid species (*Echinotiara perebaskinei* and *Glyphocyphus hattaensis*) represent only 3.2% of the total collection each, and the the the most common spatangoid (*Mecaster victori*) and holasteroid (*Hemipneustes persicus*) represent a mere 1.6% and 1.4% respectively of the total collection.

ECHINOID PALAEOECOLOGY

Echinoids are adapted to live in a wide range of habitats and the relationship between skeletal structure, habitat and mode of life is now relatively well understood. Consequently they are an excellent group to use as palaeoenvironmental indicators. Virtually nothing is known about the late Cretaceous palaeoecology of echinoids in tropical carbonate shelf environments, and the Oman Mountains collection described here provides the first such opportunity to assess echinoid distribution and faunal associations quantitatively.

Before discussing the assemblages that can be recognized and their palaeoenvironmental setting, it is necessary to look at the detailed functional morphology of the different taxa. Each has a preferred habit and life-style that is partially reflected and can be deduced from the skeletal morphology (e.g. Smith 1984).

1. *Regular echinoids*. All regular echinoids live epifaunally, but can be differentiated into a number of ecological groups based on their skeletal morphology.

(a) Hard-ground dwellers living within the zone of active wave surge (0–5 m depth). This includes *Codiopsis*, *Phymechinus*, *Circopeltis* and *Echinotiara*. These forms are characterized by their flat oral surface and enlarged phyllodes composed of P3/P4-type pore-pairs (Smith 1978). They also typically have dense or modified aboral pore-pairs indicative of specialized respiratory tube-feet. The broad, flat base and numerous, large oral tube-feet are features characteristic of present-day echinoids living on rocky surfaces within the zone of active wave surge. Large and strong oral tube-feet are necessary to provide adhesion in a turbulent environment. Modern analogues would be *Arbacia*, *Anthocidaris*, *Heliocidaris* or *Stomopneustes*, all of which are coastal species living within the first few metres on rock or other hard ground surfaces. They are rock grazers, feeding on filamentous or fleshy algae which they obtain by rasping hard substrata.

(b) Hard-ground dwellers living subtidally within the top few metres of water but subject to limited wave surge only. Here I include only *Goniopygus*. *Goniopygus* has moderately strong phyllodes, a depressed profile though without a broad flat oral surface, and well-developed aboral respiratory tube-feet (to judge from its pore-pairs). The aboral respiratory tube-feet suggest it had a relatively high metabolic rate and therefore lived in the shallow, warmest waters. It had strong oral tube-feet for adhesion, but these were not as highly developed as those of species in group (a) and it seems unlikely that *Goniopygus* could have lived in fully exposed habitats.

(c) Shallow water (*ca.* 2–10 m) forms living in more protected environments, within wave base, but not subject to strong currents or wave surge. These echinoids might typi-
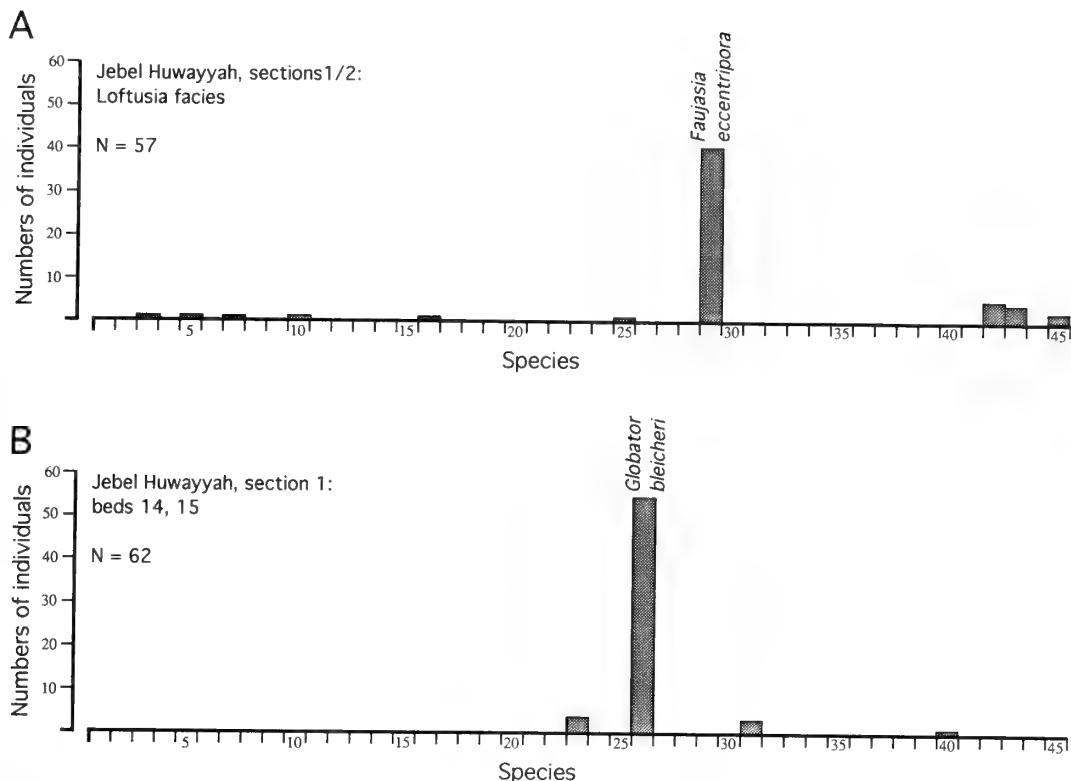
Fig. 2 Echinoid species abundances within specific units at Jebel Huwayyah. **A**, fauna from beds 10–12, section 1 and beds 1–6, section 2 (*Loftusia*-rich facies). **B**, fauna from beds 14 and 15, section 1. Species are listed numerically along the x-axis as in Table 1. N = total number of specimens collected.

cally be expected to have lived on or close to firm bottoms, i.e. either rocky or reefal knolls or stabilized sedimentary substrata. Taxa included here are *Orthopsis*, *Phymosoma*, *Plistophyma*, *Actinophyma*, *Mimiosalenia*, and *Glyphop-neustes*. These echinoids all have a depressed profile and slight phyllodes, and often have increased densities of aboral pore-pairs, possibly specialized for gaseous exchange. Their spines are moderate to long. Modern equivalents, such as *Lytechinus* or *Temnopleurus* live in and around hardground substrata in reasonably well-protected habitats. They are predominantly grazers, feeding on encrusting or boring algae or plants and removing upright algae down to the substratum. Those with no phyllode development and invaginated peris-tomes are likely to have been grazers, whereas those with oral phyllodes and a flat peristome were probably raspers.

Heterodiadema is a large, motile diadematoid-like echinoid with long spines whose closest modern counterparts are forms such as *Centrostephanus* or *Diadema*, found living in algal turf (dense stands of filamentous algae) or in amongst thick-ets in the reef flat environment (Birkeland 1989).

The cidarids *Rhabdocidaris* and *Prionocidaris* probably belong to this category. They are clearly shallow-water forms because of their well-developed respiratory tube-feet (conju-gate pore-pairs), but are globular in profile and lack phyl-lodes. They would have been confined to the most protected of the shallow-water habitats, along with *Heterodiadema*. Cidarids and diadematoids are rather generalist feeders, preferentially grazing on animals and plants, but also able to take up bottom material (Birkeland 1989).

(d) Protected subtidal (10 m plus) soft-bottom substrata

below active wave base. *Noetlingaster*, *Hattopsis* and *Salenia* are all globular forms lacking aboral specialised respiratory tube-feet. *Noetlingaster* closely resembles the present-day *Echinus* or *Tripneustes* in morphology and presumably lived in much the same way, found largely on sandy substrata of lagoons or below active wave-base moving over stable sedi-mentary bottoms or living within algal stands. These forms are predominantly herbivorous browsers, cropping exposed algae and taking loose bottom material. The extreme globu-lar shape of *Hattopsis* is matched by that seen in some present day temnopleurids such as *Microcyphus* and, like those echinoids, it may have lived within algal turf, attached to and enveloped by fronds of filamentous algae.

Irregular echinoids. These too can be divided into a number of discrete ecological groups based on observed skeletal characteristics.

(e) Infaunal medium-fine sand-grade burrowers which are selective deposit feeders using penicillate tube-feet around the mouth to pick up food particles from sediment of the burrow floor. Here I include *Hemiaster* and *Mecaster*. Both have globular tests with no real frontal sulcus. Pore differen-tiation shows that funnel-building tube-feet would have been present in ambulacrum III adapically, and subanally in the posterior ambulacra also. These heart urchins clearly lived infaunally within relatively poorly permeable, rather fine-grained sediment. An apical funnel is required by infaunal spatangoids living in finer-grained sediments, as is the aboral fasciole (which is essential for maintaining a water-filled space surrounding the test). The lack of specialization of the
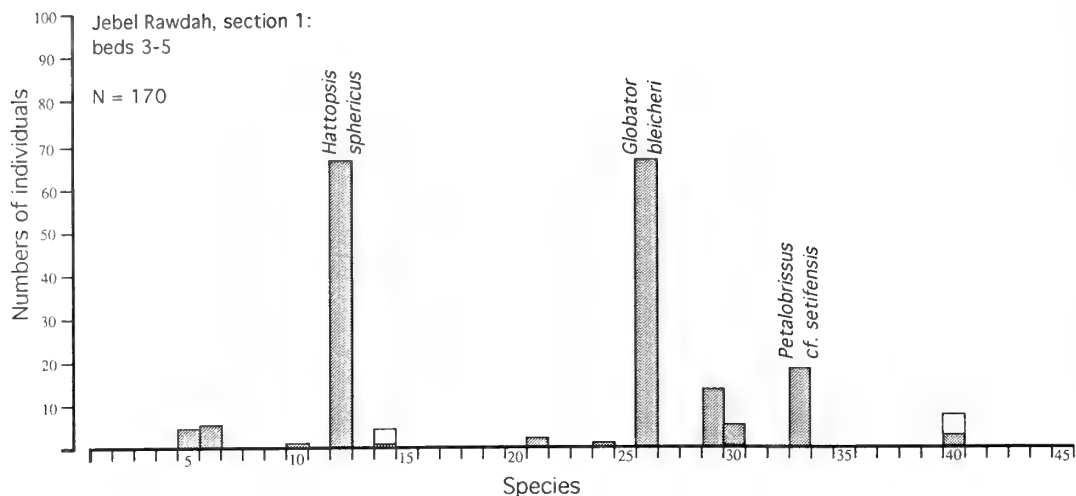
Fig. 3 Echinoid species abundances within beds 3–5 at Jebel Rawdah, section 1. Species are listed numerically along the x-axis as in Table 1. N = total number of specimens collected. Unshaded box = fragments only.

frontal groove implies that all food particles were derived from within the sediment, not from the sediment/water interface.

(f) Infaunal medium-fine sand-grade burrowers, selective deposit feeders harvesting organic material from the sediment-water interface. Only *Proraster* falls into this group. It has a deep, highly specialized frontal groove which is characteristic of those modern taxa feeding by means of a mucus-string. It is very similar to the extant *Schizaster*, and presumably lived in very much the same way. The pore-pairs in ambulacrum III are specialized and indicate the presence of highly developed funnel-building tube-feet. There is little doubt that *Proraster* lived infaunally, feeding on detritus from the water/sediment interface that cascaded down the funnel. The implication (though untested as far as I am aware) is that *Proraster* is adapted for life in more organic-poor sediments than either *Hemiaster* or *Mecaster* since it preferentially harvests surface detritus. The well-developed petals show that *Proraster* was still a relatively shallow-water form.

(g) Shallow infaunal or semi-infaunal ploughers in stable, unconsolidated bottoms. Bulk deposit feeders harvesting sediment at or close to the water interface. Only *Hemipneustes* falls into this catagory. *Hemipneustes* has a well-developed anterior groove with specialized grill spines and tube-feet. Sediment would have entered the frontal groove adapically and passed to the mouth via a mucous string running down ambulacrum III. The lack of protection for petal tube-feet, and the asymmetry of the petals implies that the surrounding sediment was highly permeable and that the urchins lived only relatively shallowly burried.

(h) Mobile high permeability (low fines) unconsolidated

medium-coarse sands: infaunal bulk sediment swallowers. This category includes *Petalobrissus*, *Nucleopygus*, *Pygurostoma* and *Stigmatopygus*. These urchins most closely resemble the present day *Apatopygus*, which is a bulk sediment swallower. They have small phyllodes around the peristome, with moderately well developed bourrelets (specialized regions of dense spines used for manipulating sand-grade particles into the peristome). Their large periproct and anal sulcus suggests they had to cope with copious faecal discharge. They are small, depressed forms streamlined for moving through loose sediment and have well-developed petals.

Vologesia and *Arnaudaster* have similar phyllodes but are much larger animals, more closely resembling *Echinolampas*. *Echinolampas* is found today in subtidal (5–20 m) depths living infaunally in shell-sands (e.g. Thum & Allen 1975). *Petalobrissus* is likely to be adapted for more mobile sediments, i.e. for shallow subtidal shoals.

(i) Mobile, permeable unconsolidated sands: selective, infaunal deposit feeders. Here I place *Zuffardia* and *Faujasia*. Both have small peristomes, surrounded by moderately well-developed phyllodes, and with slight bourrelet development. They both have rather small, posteriorly placed periprocts, and from this it would appear that they were rather more selective deposit feeders than *Petalobrissus* and other related taxa. They have large petals and clearly lived infaunally, because of their rounded shape. However, they could only have done so within highly permeable sands, finer sediments being insufficiently porous to allow sufficient water flow past the well-developed petals.

(j) Infaunal selective particle feeders living within coarse,
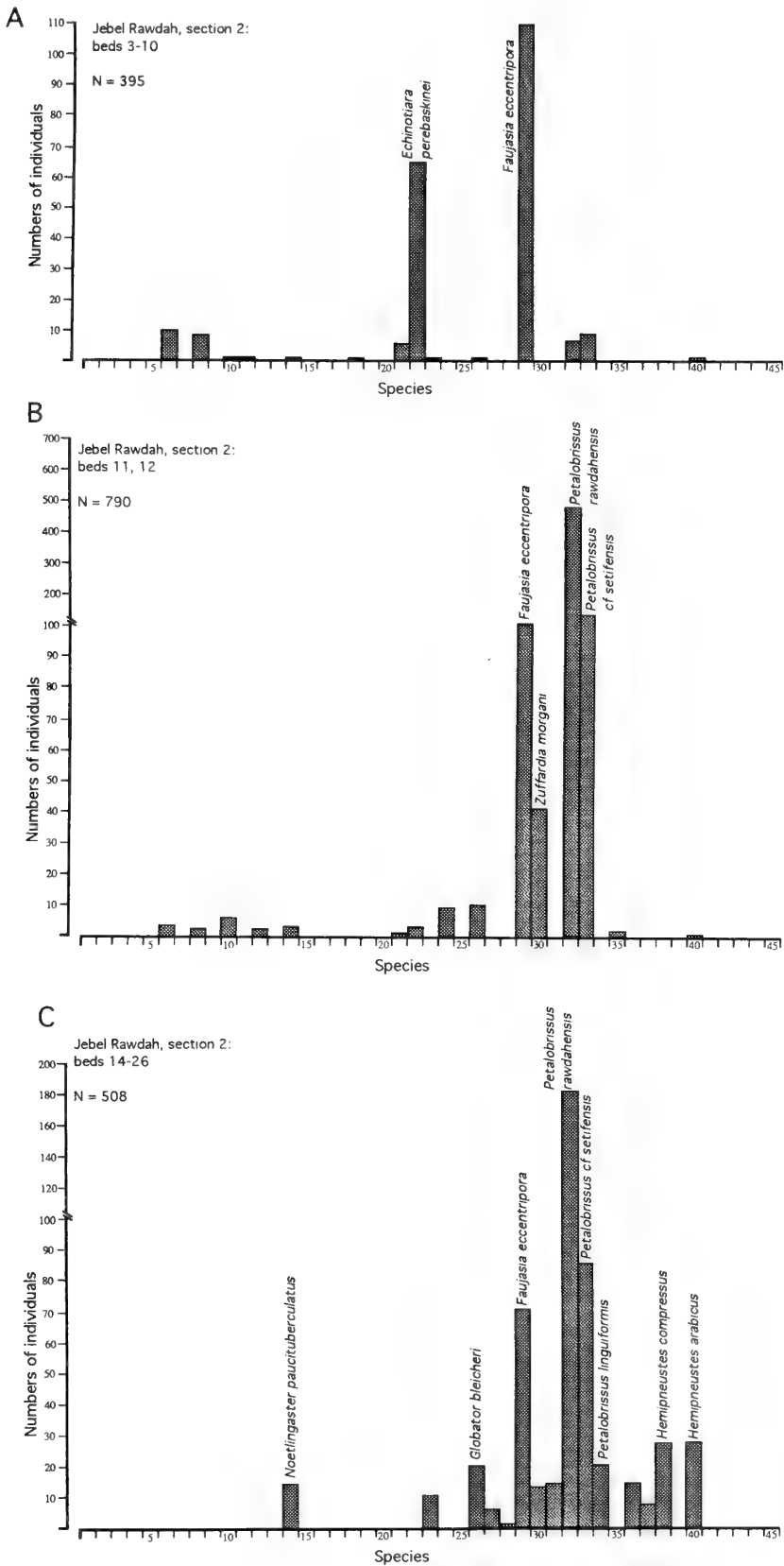
Fig. 4 Echinoid species abundances within units at Jebel Rawdah, section 2. **A**, fauna from beds 3–10; **B**, fauna from beds 11 and 12; **C**, fauna from beds 14–26. Species are listed numerically along the x-axis as in Table 1. N = total number of specimens collected.

Table 2   Inferred palaeoenvironmental settings for the late Cretaceous succession of the Oman-United Arab Emirates border region. The common echinoid taxa found in each habitat are listed, together with indications of their probable life style.

Habitat A   nearshore hardground dwellers living in zone of active wave surge.
 (i) Hardground grazers: *Echinotiara perebaskinei*, *Phymechinus? perplexus*, *Codiopsis lehmannae*.

Habitat B   nearshore hardground dwellers living in more protected environments (perireefal).
 (i) Hardground grazers: *Goniopygus arabicus*.

Habitat C   subtidal protected environments within normal wave base; mixed cobble and sand substrata with nearby level-bottom reefal thickets.
 (i) Epifaunal grazers: *Glyphopneustes hattaensis*, *Mimiosalenia quinquetuberculata*, *Goniopygus arabicus*, *Phymosoma hexoaporum*.
 (ii) Epifaunal browsers: *Circopeltis? emiratus*, *Heterodiadema buhaysensis*, *Orthopsis miliaris*, *Hattopsis paucituberculatus*, *Plistophyma asiaticum*.
 (iii) Epifaunal generalists: *Prionocidaris morgani*, *Prionocidaris? emiratus*, *Salenia nutrix*, *Salenia microprocta*.
 (iv) Infaunal grazers/detritivores: '*Globator*' *bleicheri*, *Conulus douvillei*, *Coenholectypus* cf. *baluchistanensis*.
 (v) Infaunal bulk sediment swallowers: *Nucleopygus magnus*, *Pygurostoma morgani*.
 (vi) Infaunal selective deposit feeders: *Vologesia rawdahensis*, *Arnaudaster cylindriformis*, *Hemiaster hattaensis*.

Habitat D   Shore-face sand flats at or within normal wave base.
 (i) Bulk sediment swallowers: *Petalobrissus rawdahensis*, *P.* cf. *setifensis*.
 (ii) Selective deposit feeders: *Zuffardia morgani*, *Faujasia eccentripora*.
 (iii) Infaunal generalist detritivores: '*Globator*' *bleicheri*, *Coenholectypus* cf. *baluchistanensis*.

Habitat E   Broad shallow, open shelf subtidal sand flats, within normal wave base (2–10 m) but distant from the platform margin and thus relatively protected.
 (i) Epifaunal grazers: *Noetlingaster paucituberculatus*, *Hattopsis sphericus*.
 (ii) Semi-infaunal selective deposit feeders: *Hemipneustes* spp.
 (iii) Infaunal selective deposit feeders: *Mecaster victoris*, *Hemiaster paronai*, *Stigmatopygus? pulchellus*, *Faujasia eccentripora*.
 (iv) Infaunal bulk sediment swallowers: *Petalobrissus rawdahensis*, *P.* cf. *setifensis*, *Pygurostoma morgani*.

Habitat F   Deeper-water (20 m plus) platform basinal muddy sands, below normal wave base.
 (i) Epifaunal grazers: possibly *Actinophyma spectabile*.
 (ii) Infaunal selective deposit feeders, harvesting detritus from the sediment/water interface: *Proraster geayi*.

permeable sands behind fringing reefs in 0–10 m water depth. *Conulus*, '*Globator*' and *Coenholectypus* belong here, though the highly inflated *C. inflatus* may have reverted to a primarily epifaunal mode of life, below normal wave base. *Globator* closely resembles the present day *Echinoneus* whose ecology was described by Rose (1976). *Echinoneus* lives beneath coral debris in coarse shell-sands passing suitable grains into its peristome by means of its tube-feet.

Inferred depths and habitats for typical Omani echinoids are tabulated in table 2.

ECHINOID ASSEMBLAGES

Because careful count of the number of specimens collected for each taxon was kept it is possible to identify recurring assemblages. The following seven assemblages are differentiated here.

(1). Conulid/arbacioid assemblage. An abundance of *Conulus* and '*Globator*' which is usually accompanied by a diverse mixture of regular echinoids, notably by the arbacioids *Goniopygus*, *Glyphopneustes*, *Mimiosalenia* and *Hattopsis*. Other taxa making up a smaller component of the fauna include *Phymosoma*, *Nucleopygus* and *Pygurostoma* (Figs 2B, 3, 5B, 6).

This assemblage is characteristic of the lower beds of the Simsima Formation at Jebel Buhays, Jebel Thanais, Jebel Faiyah, and Jebel Huwayyah. It is typically developed with the income of relatively coarse, carbonate bioclastic sands in the succession.

Interpretation: the conulid/arbaciid assemblage has a very high diversity of regular echinoids that would have preferred stabilized bottoms in shallow water conditions protected from the influence of strong wave action. The presence of '*Globator*' implies that the sediment was unconsolidated, permeable and rather coarse, while horizons with an abundance of *Hattopsis* might suggest the presence of nearby algal stands. The abundance and diversity of regular echinoids (most of which are algivore grazers) implies a mixture of environments were close by, ranging from rocky (?patch-reef, as seen at Jebel Faiyah) to stabilised sedimentary bottoms with algal stands. The palaeoenvironment is therefore most likely to represent a shallow (5–10 m) backreef or leaward environment that supports a high algal diversity.

(2). *Echinotiara/Faujasia/Phymechinus* assemblage. An assemblage which includes a number of rarer regular echinoids absent from most other assemblages (e.g. *Codiopsis*, *Phymechinus*). *Faujasia* is the only common element found at other levels, but no other irregular echinoid occurs in any abundance (Fig. 4A).

This assemblage is best developed at Jebel Rawdah section 2, in the basal calcarenitic beds with associated coral/rudist debris.

Interpretation: this assemblage is dominated by hardground, shallow-water (0–5 m) epifaunal regular echinoids (*Echinotiara*, *Phymotaxis*, *Codiopsis*) adapted for life in strong wave-surge environments. Clearly none are preserved in situ, but have been transported into immediately adjacent basins of sediment accumulation, along with coral and stromatoporoid debris and hippuritid rudist debris indicative of reef habitat. Transportation has not been far, otherwise much more disintegration of tests might be expected. The occurrence of large blocks of rolled coral with stromatoporoid and rudist debris at Jebel Rawdah section 3, implies that the deposits accumulated close to actual reefal framework. *Fauja-*
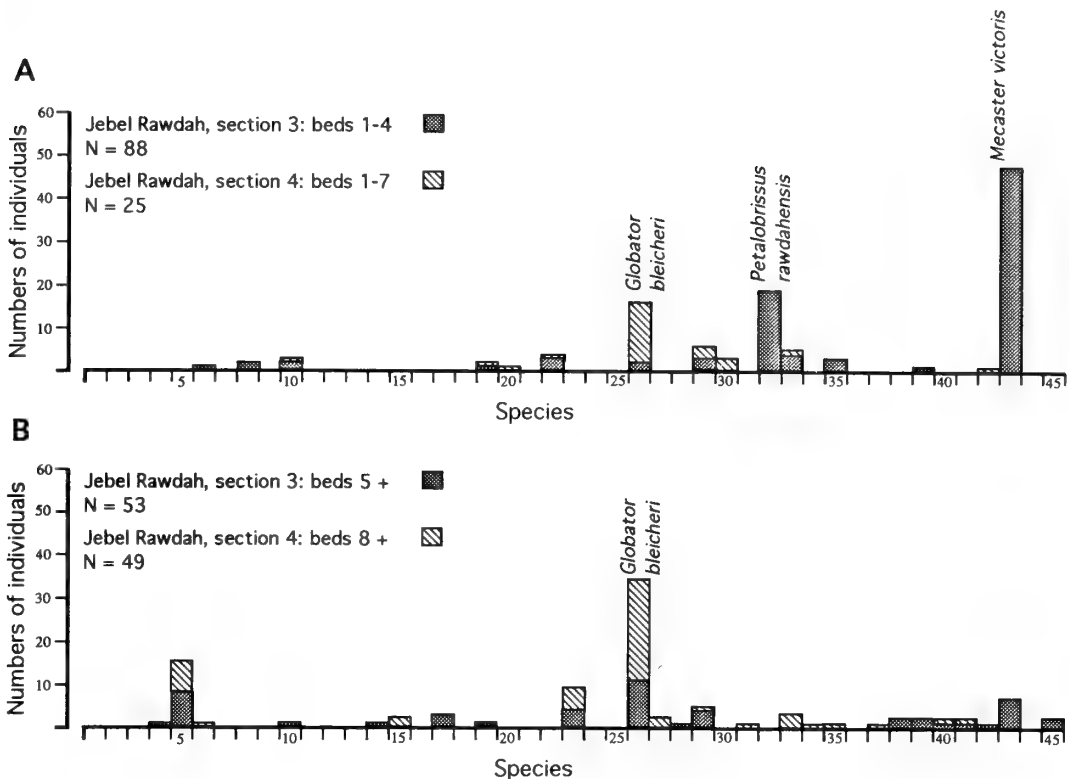
Fig. 5 Echinoid species abundances within units at Jebel Rawdah, sections 3 and 4. **A**, fauna from lower beds; **B**, fauna from higher beds. Species are listed numerically along the x-axis as in Table 1. N = total number of specimens collected.
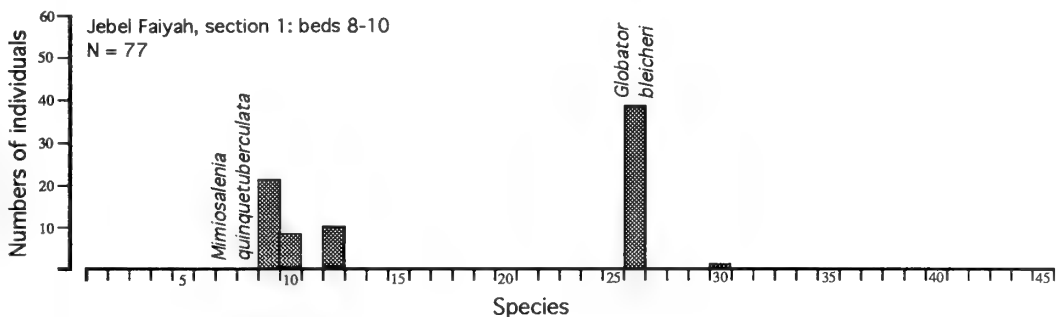
Fig. 6 Echinoid species abundances within units at Jebel Faiyah, section 1, beds 8–10. Species are listed numerically along the x-axis as in Table 1. N = total number of specimens collected.

a may be the only in situ echinoid for the depositional environment, living within the surrounding sand-fields in an immediately subtidal environment, although none is preserved with associated spines. *Goniopygus* is found in association, and it probably lived amongst the tallus derived from the reef crest rather than on the crest itself.

) *Petalobrissus* assemblage. At certain levels of coarse, inconsolidated orbitoline limestones *Petalobrissus* occurs in large abundance, accompanied by much smaller numbers of other infaunal echinoids (*Zuffardia, Faujasia, Coenholectypus* and '*Globator*'). Rare *Noetlingaster* are the only regular echinoids encountered (Fig. 4B).

This assemblage is seen only in the lower part of the section (beds 11–13) at Jebel Rawdah, section 2.

Interpretation: this assemblage is composed entirely of small, bulk sediment swallowers and is suggestive of shallow subtidal unconsolidated and well-washed sand flats free of algae, presumably subject to constant disturbance. The beds can thus be envisaged as shallow (0–10 m) orbitoline sand flats developed behind a fringing reef. The abundance of individuals suggests that this was a region of relatively high productivity.

(4) *Hemipneustes/Noetlingaster* assemblage. The abundance of large infaunal selective deposit feeders, notably *Hemip-*

neustes and *Pygurostoma*, characterises this assemblage. Usually *Noetlingaster*-rich levels alternate with holasterid-rich levels, so it may not be entirely correct to treat these as one assemblage, though they occur intermixed within the same lithofacies. All the species are large in comparison to those elsewhere. This assemblage typifies the upper beds of section 2, Jebel Rawdah (Fig. 4C).

Interpretation: the *Hemipneustes*/*Noetlingaster* assemblage is composed of selective deposit feeders specialized for life within coarse, permeable sands, together with occasional specific bands of the large generalist algivore *Noetlingaster*. The dominance of large selective deposit feeders implies a relatively nutrient-starved environment where large-scale harvesting of the sediment/water interface is needed to exploit the food supply. Associated lithofacies evidence suggests that they were living within shallow-water (2–10 m) flat-bottom shoals, probably immediately infratidal. *Noetlingaster*, like *Echinus* in today's seas, may have been a generalist detritivore/algivorous browser. The environment of deposition is therefore envisaged as relatively quiet sedimentary level bottom shoals that lay not particularly deep but distant from the high productivity reef area or from more exposed platform margin conditions.

(5) *Faujasia* assemblage. Occasional, almost monospecific assemblages of *Faujasia* are found in calcified fine sands at Jebel Huwayyah near the base. In the associated *Loftusia*-rich levels there are also occasional *Hemiaster* and *Proraster*. These may be nearshore infratidal sands in relatively protected environments (Fig. 2A).

(6) *Mecaster* assemblage (Fig. 5A). Another virtually monospecific assemblage confined to a single level at Jebel Rawdah section 3. This time the only associated echinoids are the rare *Hemipneustes*.

(7) *Proraster* assemblage. Only *Proraster* is found in the highest, muddiest limestones of Jebel Huwayyah. The relatively fine-grade sediments and the absence of infaunal cassiduloids or holasteroids suggests that these beds may represent shelf-basinal deposits more than *ca.* 20 m deep. Only highly specialist infaunal forms such as *Proraster* could apparently cope with life in these relatively nutrient-poor mud-rich deposits.

PALAEOECOLOGICAL SYNTHESIS

The faunal succession records a relatively rapid deepening from beach boulder beds and sands through nearshore, high-energy, subtidal conditions with off-beach coral-rudist reefal patches to somewhat deeper-water conditions at or immediately beneath wave base. Maximum echinoid diversity is found in the shallow sand fields strewn with shell and coral debris surrounding coral thickets that formed at about wave-base around the shores of the uplifted ophiolite. Subsequent shallowing over the platform led to the creation of broad, shallow shoals supporting a low-diversity infaunal echinoid assemblage, dominated by holasteroids and cassiduloids. The only epifaunal echinoid here is *Noetlingaster*. The deepest water facies are probably those seen at the top of the section at Jebel Huwayyah, where only the infaunal spatangoid *Proraster* occurs.

SYSTEMATIC DESCRIPTIONS

Class **ECHINOIDEA** Leske, 1778
Subclass **CIDAROIDEA** Claus, 1880
Order **CIDAROIDA** Claus, 1880
Family **RHABDOCIDARIDAE** Lambert, 1900

Gen. et sp. indet.   Pl. 1, fig. 1; Fig. 8

MATERIAL. A single specimen, comprising three interambulacral plates, BMNH EE3438.

OCCURRENCE. From the scree at Jebel Buhays, section 1; derived from the lowest 2–3 metres of the Simsima Formation.

DESCRIPTION. Three interambulacral plates, rather badly weathered, from the ambital region of the test. Plates are 18·7 mm wide by 8 mm tall and appear to have tesselate sutures. Each plate carries a single large tubercle with a circular, confluent areole that occupies the full height of the plate. The boss is surmounted by a broad, strongly crenulate

Lithofacies 4

Well-sorted orbitoid-rich packstones

Hemipneustes spp.
Coenholectypus inflatus
Pygurostoma
Stigmatopygus
Noetlingaster

Lithofacies 3b

Poorly-sorted orbitoid-rich packstones with rhodolites and *Dictyoptychus*

Petalobrissus spp.
Zuffardia

Lithofacies 3c

Muddy calcarenites: very poorly sorted. *Loftusia* and *Cunnolites* prominent.

Hattopsis
Hemiaster

Lithofacies 3a

Poorly-sorted bioclastic calcarenites

Goniopygus
Glyphopneustes
Salenia
Orthopsis
Phymosoma
Nucleopygus
Globator
Coenholectypus baluchistanensis

Bedrock

Echinotiara
Codiopsis
Phymechinus?

Shore-face clastic sands

Faujasia

Fig. 7 Schematic reconstruction of the sea-floor in Maastrichtian times showing the range of environments represented in the study area. Sea urchins are illustrated in their probable mode of life and the inferred environmental ranges for key taxa are shown.
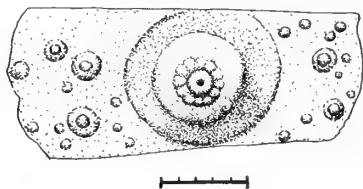
Fig. 8 Camera lucida drawing of an interambulacral plate of Rhabdocidaridae gen. et sp. indet., BMNH EE3438. Scale bar = 5 mm.

platform while the mamelon itself is rather small (1·2 mm diameter) and has a large central perforation. The primary tubercle lies subcentrally on the plate with a broad adradial and interradial platform on either side. The broad zones outside the areole of the primary tubercle have a few scattered secondary tubercles preserved, but are otherwise too abraded to retain any evidence of fine tuberculation that may have been present. It is clear from the distribution of the tubercles that are preserved that these regions were covered in a rather heterogenous and open array of various-sized tubercles.

REMARKS. The broad plates, confluent areoles, perforate crenulate tubercles and heterogeneous secondary tuberculation show this to be a member of the Rhabdocidaridae. It is impossible to place this specimen in any genus on the basis of such incomplete material. However, it most probably represents a species of *Rhabdocidaris* itself, judging from the size of the specimen and the coarseness of the secondary tuberculation.

Family **CIDARIDAE** Gray, 1825
Tribe **CIDARINI** Gray, 1825
Subtribe **PHYLLACANTHINA** Smith & Wright, 1989
Genus *PRIONOCIDARIS* Agassiz, 1863

Prionocidaris morgani (Gauthier, 1902) Pl. 1, figs 2–4; Fig. 9B

1902 *Rhabdocidaris (Leiocidaris) morgani* Gauthier: 145, pl. 20, figs 3–6.
1989 *Cidaris* cf. *scabra* Gauthier; Ali: 398, fig. 2.1.

TYPES. The syntypes are the two specimens described and figured by Gauthier. One is a more or less complete test 35 mm in diameter, the other an interambulacral segment. The whereabouts of this material is unknown: the specimens are

not in the Morgan collection in the Museum National d'Histoire Naturelle, Paris.

MATERIAL STUDIED. Two specimens: BMNH EE3433, from the scree derived from the lowest beds of the Simsima Formation at Jebel Buhays, section 1; BMNH EE3435, loose in the scree at section 3b, Jebel Rawdah. A third fragment, EE3434, probably belonging to this species, was also found loose in the scree at Jebel Buhays.

OCCURRENCE. The syntypes come from the late Cretaceous ('Senonien superieur') of Louristan, Iran (Gauthier was unable to give a precise locality). In the United Arab Emirates the species comes from the Maastrichtian of Jebel Buhays and Jebel Rawdah.

DIAGNOSIS. A species of *Prionocidaris* with broad conjugate pore-pairs occupying more than half of the ambulacral plate width, and a perradial zone with a single primary tubercle and a row of tubercle-like granules, up to four abreast, on each plate. Interambulacra with well differentiated scrobicular circles and aligned extrascrobicular tuberculation.

DESCRIPTION. The following description is based on BMNH EE3433, the larger and better preserved of the two. The specimen comprises parts of two interambulacra and ambulacra. Interambulacral width at the ambitus is 23 mm, suggesting a test diameter of approximately 50 mm in life. Test height is 32 mm. The ambulacra are 6 mm in width and only slightly sinuous. The pore-pairs are very wide and conjugate (Pl. 1, fig. 4; Fig. 9B) and successive pore-pairs are closely spaced. The poriferous zone occupies approximately half of the plate width. There is a single primary tubercle with a mamelon immediately adjacent to each pore-pair. The remainder of the perradial zone is occupied by a row of large granules (non-mamelonate), some three or four abreast and organised into discrete vertical rows.

Interambulacral plates are relatively broad, an ambital plate being 13·1 mm by 9·4 mm in height. All plates, except the most adapical in each column, have a single large primary tubercle. This has a sunken areole 7·2 mm in diameter and a mamelon 2.2 mm in diameter (Pl. 1, figs 2, 4). Mamelons are perforate and the surrounding platform is non-crenulate. The primary tubercles lie offset towards the adradial suture leaving a broad interradial zone of miliary tuberculation. There is a clearly differentiated ring of scrobicular tubercles surrounding each areole. Extrascrobicular tuberculation is well developed with approximately 2 miliary granules abreast towards the adradial suture, eight abreast towards the interradial suture, and either a single row or no row developed adapical and adoral to the scrobicular circles. These extra-scrobicular tubercles are non-mamelonate and decrease in size towards
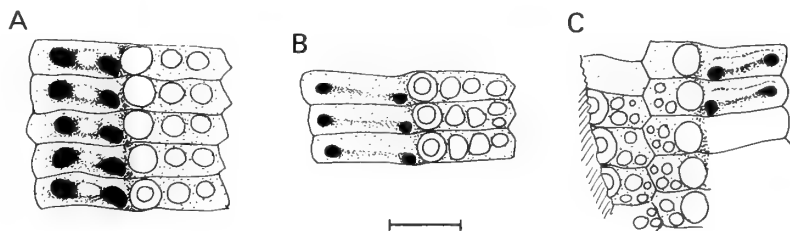
Fig. 9 Camera lucida drawings of ambital ambulacral plating in cidarid species. **A**, *Stereocidaris persica* (Cotteau & Gauthier), Museum d'Histoire Naturelle, Morgan Collection; **B**, *Prionocidaris morgani* (Gauthier), BMNH EE3433; **C**, *Prionocidaris? emiratus* sp. nov., BMNH EE3431. Scale bar = 1 mm.
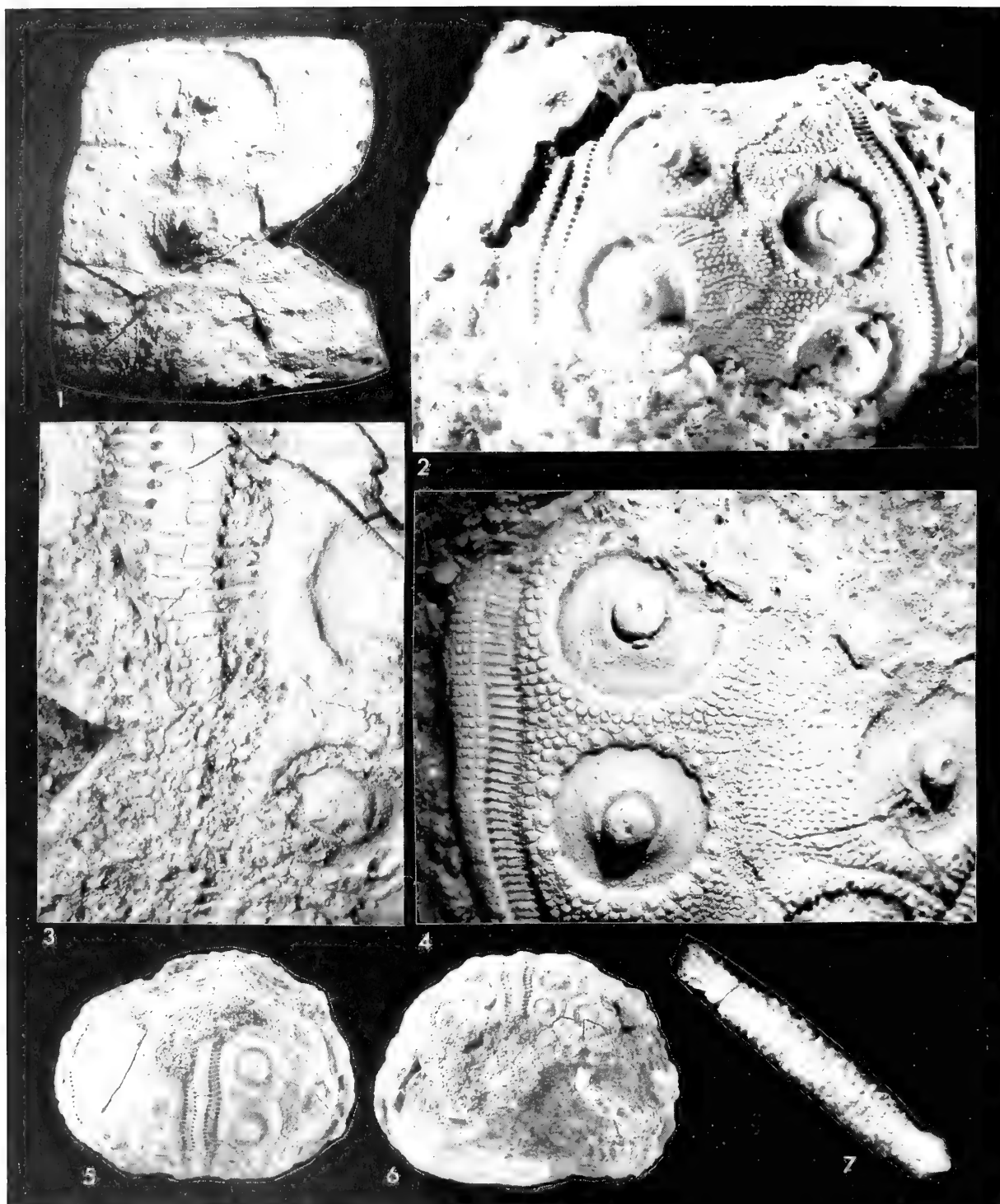
Fig. 1   Rhabdocidarid gen. et sp. indet. BMNH EE3438; three interambulacral plates, × 3. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation.

Figs 2, 4   *Prionocidaris morgani* (Gauthier). BMNH EE3433. **2**, adapical portion of interambulacrum and adjacent ambulacral zones, × 2·5; **4**, interambulacrum detail, × 4·5. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation.

Figs 3, 5, 6   *Prionocidaris? emiratus* sp. nov. BMNH EE3431, holotype. **3**, ambulacral zone detail, × 10; **5**, lateral, × 2; **6**, oral, × 2. Jebel Huwayyah, section 2, beds 3–6.

Fig. 7   Cidarid spine, possibly belonging to *Prionocidaris morgani* (Gauthier). BMNH EE3434, × 3. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation.

the interradius. There are neural grooves developed in the extra-scrobicular regions.

The smaller specimen (BMNH EE3435) is more complete, but less well preserved. It has seven interambulacral plates in a column at an estimated test diameter of about 35 mm. Adapical interambulacral plates retain fully formed tubercles.

Two cidarid spines were also collected from the scree at Jebel Buhays and probably belong to this species. The best preserved is BMNH EE3434 (Pl. 1, fig. 7). It is 19 mm long by 2·6 mm wide. It has a short neck and a perforate, non-crenulate base. The shaft is widest midlength and tapers towards the tip, but then expands slightly at the very tip to end in a blunt crown. The shaft is covered in rows of thorns which coalesce to form ribs towards the tip.

REMARKS. This species differs from the most common late Cretaceous cidarid described from Iran, 'Cidaris' persica Cotteau & Gauthier (1895), in having much finer and denser extra-scrobicular tuberculation and wider and more strongly conjugate pore-pairs at a comparable size (compare Figs 9A, B). 'C'. persica belongs to the genus Stereocidaris and has a characteristic strong interporal ridge developed between pore-pairs. Cidaris scabra Gauthier (1902) was established for a 30 mm diameter individual of uncertain provenance within Louristan. It differs primarily in having two ambulacral tubercles to each plate but has very similar strongly conjugate pore-pairs. Ali (1989) described a specimen of P. morgani from Jebel Rawdah under the name Cidaris cf. scabra Gauthier.

Spines comparable in morphology to the one described here have previously been described under the name Cidaris aftabensis Gauthier (1902). They can only tentatively be assigned to this species until specimens are found that are attached to a test.

Prionocidaris? emiratus sp. nov. Pl. 1, figs 3, 5, 6; Fig. 9C

TYPE. Holotype and only known specimen, BMNH EE3431.

OCCURRENCE. Found loose in the *Loftusia* levels a little below Beds 6/7, section 2, Jebel Huwayyah.

DIAGNOSIS. A cidarid with conjugate ambulacral pore-pairs and a single primary ambulacral tubercle to each plate, adjacent to the pore-pair. The perradial zone of each ambulacrum is filled with small, dense miliary tuberculation, three or four to a plate and arranged in two rows.

DESCRIPTION. Test 28·5 mm in diameter by 18·9 mm in height. Ambulacra 3·6 mm in width at the ambitus, slightly sinuous. Pore-pairs strongly conjugate, with individual pores of each pair ca. 0·3 mm diameter and separated by an interporal distance of about 0·7 mm (Pl. 1, fig. 3; Fig. 9C). Perradial zone elevated and more or less flat; comparatively short and tall. A large primary tubercle occupies about half of the tuberculate region on each plate (Pl. 1, fig. 5; Fig. 9C). These tubercles are almost contiguous vertically. The central part of the perradial zone is occupied by very much smaller granules, some three or four to a plate, irregularly scattered.

There are six interambulacral plates in a column, of which the most adapical in each zone has only a rudimentary tubercle. Ambital plates are relatively tall and narrow, 7·0 mm wide and 5·8 mm high (Pl. 1, fig. 5). The primary tubercle lies centrally on the plate and has a sunken areole 4 mm in diameter (on ambital plates). The mamelon (1·1 mm

in diameter) is perforate and non-crenulate. The surrounding scrobicular circles are non-contiguous. Extra-scrobicular tuberculation is very fine and dense. There are approximately three to four granules abreast on the interradial margin, three abreast adapically and two abreast both adradially and adorally.

REMARKS. The strongly conjugate pore-pairs indicate that this is a member of the Phyllacanthina, and in many respects it is close to *P. morgani* in tuberculation and appearance. The interambulacra are narrower than usual for *Prionocidaris*, and the interradial zones less well developed. Therefore, it is only tentatively assigned to this genus. *P? emiratus* can be easily differentiated from *P. morgani* by its ambulacral tuberculation (compare Figs 9B and 9C). None of the cidarid species described by Cotteau & Gauthier (1895) or Gauthier (1902) have this form of tuberculation.

Indet. cidarid plates

In addition to the specimens described above, fragmentary material of cidaroids has been collected from the basal beds at Jebel Faiyah, section 1, and the *Loftusia* levels (beds 1–6) at Jebel Huwayyah. None of this material is adequate to determine to generic level.

?Order **DIADEMATOIDA** Duncan, 1889
Family **HETERODIADEMATIDAE** Smith & Wright, 1993
Genus ***HETERODIADEMA*** Cotteau, 1864

Heterodiadema buhaysensis sp. nov. Pl. 2, figs 1–3; Figs 10, 11

TYPES. Holotype BMNH EE3441; paratypes, BMNH EE3442–5, EE5019.

OTHER MATERIAL. One other specimen, BMNH EE3446.

OCCURRENCE. Five specimens come from the lowest beds of the Simsima Formation and were collected in the scree derived from the lowest few metres of that formation at Jebel Buhays, section 1. One was collected from the lowest 1·5 m of Simsima Formation at Jebel Thanais. One specimen was collected from bed 5 at Jebel Rawdah, section 3b.

DIAGNOSIS. Apical disc large, pentagonal, caducous; probably monocyclic to judge from the outline. Ambulacra trigeminate, relatively wide with diadematoid-style plate compounding. Phyllodes absent. Primary tubercles perforate, crenulate; reducing in size sharply adapically and tending to become imperforate. Broad zones of granulation along the perradius, adradius and interradius. Peristome invaginated with reasonably deep and sharply defined buccal notches with tags.

DESCRIPTION. Tests range in diameter from 18–36 mm. The test is circular in outline and depressed in profile, with a height 42–48% of the diameter (mean = 45%; Fig. 10). The ambitus lies at about mid-height and the sides are uniformly rounded (Pl. 2, fig. 3). The apical disc and peristome are slightly invaginated in the largest specimen. Coronal plates are all firmly sutured together.

The apical disc is caducous and has been lost from all specimens. The apical disc opening is pentagonal in outline with the angles projecting reasonably strongly into the interradii (slightly more into the posterior interradius, which isalso
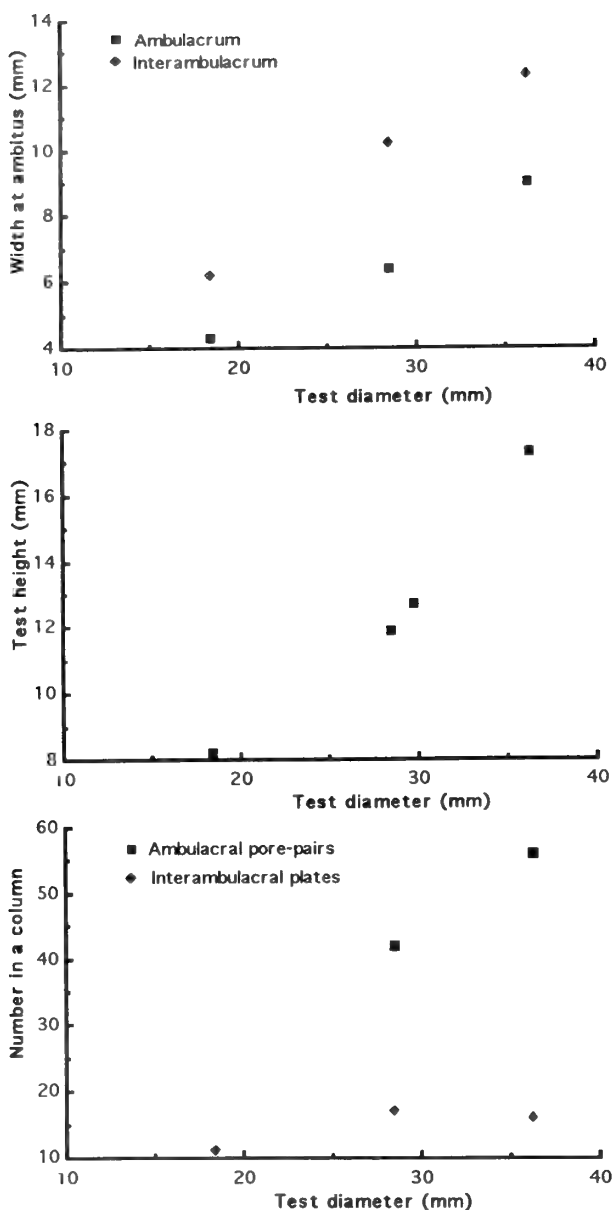
Fig. 10   Biometric data for *Heterodiadema buhaysensis* sp. nov.
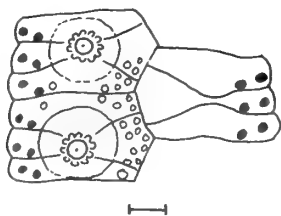
Fig. 11   Camera lucida drawing of three ambital ambulacral plates of *Heterodiadema buhaysensis* sp. nov., BMNH EE3444. Scale bar = 1 mm.

more rounded). It is a little longer than broad with a length that is 36–43% of the test length.

Ambulacra are broad and nearly parallel-sided at the ambitus but taper gradually both adapically and adorally. At the ambitus they have a width that is 23–25% of the test length. Pore-pairs are uniserial throughout, without any widening whatsoever at the peristomial margin. Plates are compound, with diadematoid-style triads in which the central element is the largest and upper and lower elements both taper towards the perradial and adradial suture (Fig. 11). Each triad bears a primary tubercle and there is a well-developed perradial band of miliary tuberculation that expands adapically. At the ambitus in the largest specimen perradial tubercles are about three abreast. Oral and ambital tubercles are perforate and crenulate, but tubercles reduce sharply in size above the ambitus, where they may become imperforate and non-crenulate (some remain perforate). This reduction in size occurs above about the seventh compound plate. Larger tubercles have circular, non-confluent areoles. At the ambitus pore-pairs are rather widely spaced and separated by a single row of miliary tubercles. There are no obvious sphaeridial pits around the peristome.

Interambulacra are about 1·3–1·5 times as wide as the ambulacra. There are 15 plates in a column at 36 mm test diameter. All plates have a single large primary tubercle that is perforate and crenulate and is surrounded by a circular areole. The mamelon is notable for its small size in comparison to the size of the areole. Areoles are non-confluent, being separated for the most part by a single band of miliaries. Tubercles decrease in size sharply towards the apex and may become imperforate. There are broad zones of uniform miliary tuberculation both adradially and interradially: about six abreast adradially and three or four abreast interradially at the ambitus in the largest specimen. Scrobicular tubercles are not differentiated.

The peristome is relatively large, 28% of test diameter in a 36 mm diameter individual. It is strongly indented by the buccal notches. There are broad, smooth tongue-like regions running adradially from each buccal notch and extending up to the fourth interambulacral plate.

REMARKS. This species is most closely related to the mid-Cretaceous (Cenomanian) *Heterodiadema lybica* (Agassiz & Desor). Both have a similar form of ambulacral compounding and a very similar tuberculation style. Granular zones are broad and well developed and in both there is a sharp reduction in the size of primary tubercles above the ambitus, with those adapically tending to become imperforate and non-crenulate. Finally, both have the distinctive tubercle-free tag to the buccal notches and uniserial pore-pairs throughout. *H. buhaysensis* differs from *H. lybica* in having fewer reduced tubercles, the primary tubercles becoming smaller considerably closer to the apex in *H. buhaysensis* in individuals of comparable size. It also differs in lacking the extreme prolongation of the apical disc into the posterior interambulacrum seen in medium to large specimens of *H. lybica*.

Heterodiadema was placed in its own family by Smith & Wright (1993). Where this family fits into the higher taxonomy of echinoids, however, is much less certain. They may be members of the aulodont group Diadematoida. This is suggested by the prominent buccal tags and the very delicate mamelons on the primary tubercles, which indicate that the species had small, fragile spines. Alternatively they may be stirodonts, early members of the Phymosomatoida (as
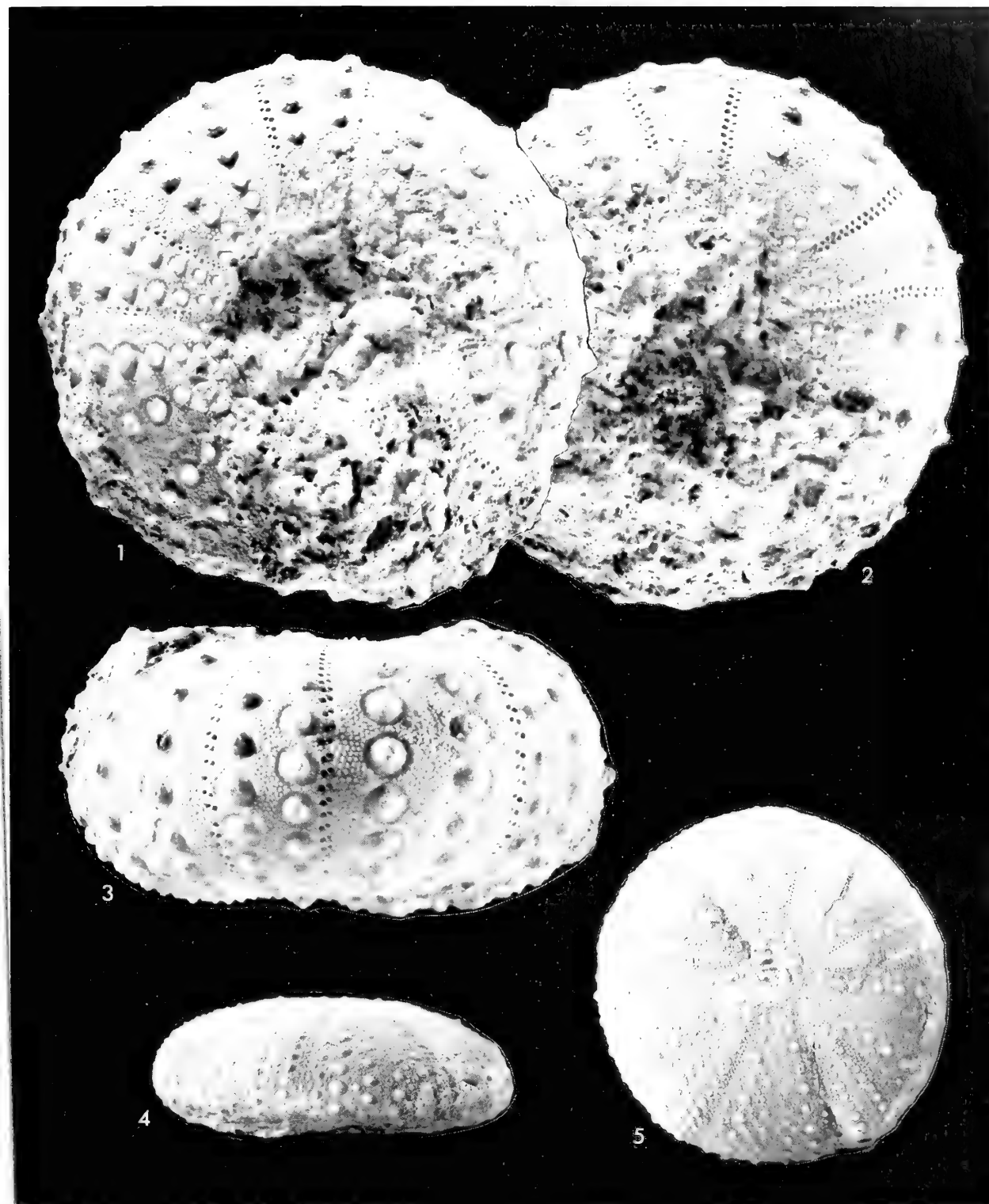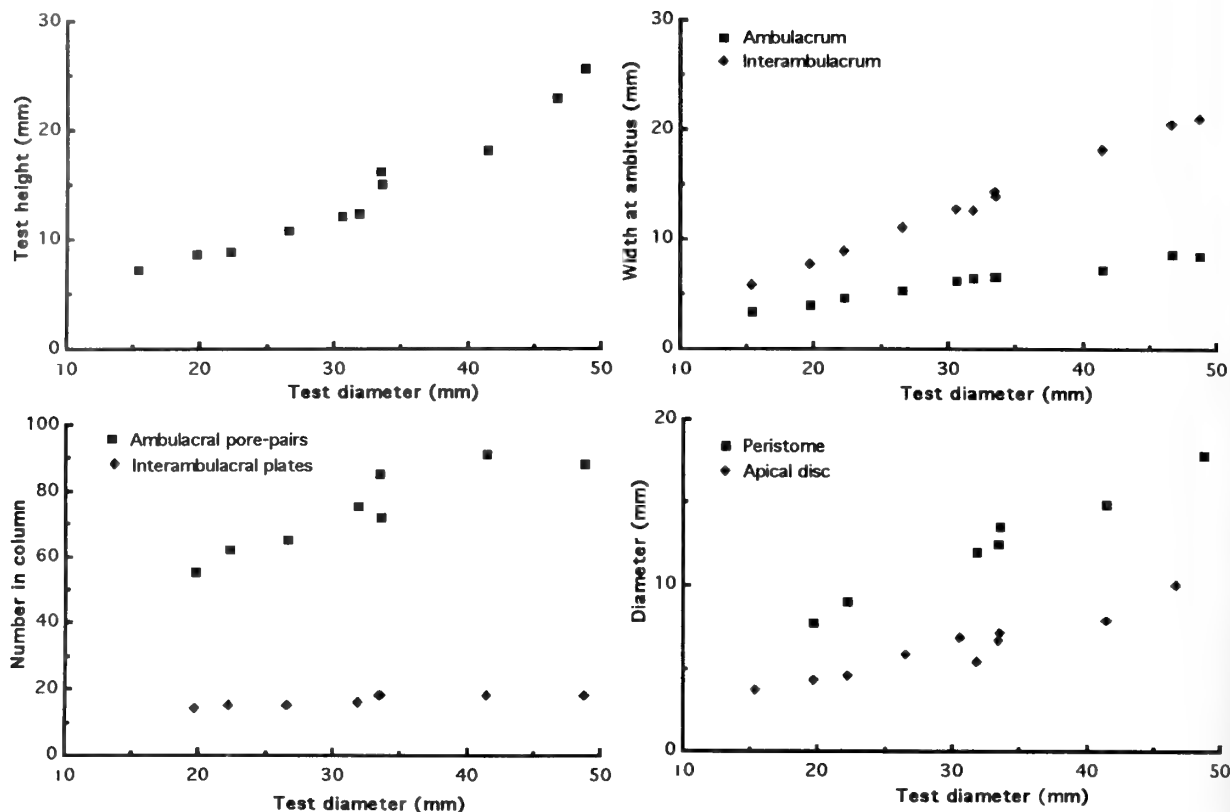
Fig. 12   Biometric data for *Orthopsis miliaris* (d'Archiac).

defined by Smith & Wright, 1993). Diadematoids and phymosomatoids are fundamentally differentiated on the structure of their spines and lantern apparatus, diadematoids having hollow spines and grooved teeth, phymosomatoids having solid spines and keeled teeth. In neither *H. lybica* nor in our new species are the spines or lantern known, thus its higher taxonomic position must remain unresolved. Because of its delicate tuberculation, it is tentatively assigned here to the Diadematoida.

Infraclass **ACROECHINOIDEA** Smith, 1984
Plesion (Order) **ORTHOPSIDA** Mortensen, 1942
Family **ORTHOPSIDAE** Duncan, 1889
Genus ***ORTHOPSIS*** Cotteau, 1864

Orthopsis miliaris (d'Archiac, 1835)   Pl. 2, figs 4, 5; Pl. 3, figs 1–9; Figs 12–14

1835   *Cidarites miliaris* d'Archiac: 179, pl. 11, fig. 8.
1895   *Orthopsis morgani* Cotteau & Gauthier: 87, pl. 14, figs 6–9.
1933   *Orthopsis sanfilippoi* Checchia-Rispoli: 6, pl. 1, figs 5–15.
1985   *Orthopsis miliaris* (d'Archiac); Geys: 143, pl. 5, figs 8–10 (see also for full prior synonymy).
1989   *Orthopsis morgani* Cotteau & Gauthier; Ali: 401, fig. 2 (7).
1991   *Orthopsis miliaris* (d'Archiac); Smith & Bengtson: 30, pl. 8B-F, text-fig. 23.

MATERIAL STUDIED. Forty seven specimens of which the following 11 were used in the biometric analysis: BMNH EE3720–21, EE3723, EE3725–26, EE3728, EE3731, EE3733, EE3738, EE3740, EE3749 and EE5018.

OCCURRENCE. In the western Oman mountains this species occurs at the following localities and horizons (numbers in brackets are number of specimens):
Jebel Buhays, section 1: loose in scree derived from lowest few metres of the Simsima Formation (13)
Jebel Thanais: lowest 2 m of Simsima Formation (1).
Jebel Huwayyah, section 2: Loftusia levels (beds 3–5; 1 fragment).
Jebel Rawdah, section 1: beds 3 and 4, and loose (4).
Jebel Rawdah, section 3b: bed 2 (1); bed 3, 1m above base (1), bed 8 (2); bed 9 (8); bed 10 (1); loose (3).
Jebel Rawdah section 4: bed 12 (5);top of bed 15 (1); loose, lower half of sandy beds (1).
Jebel Faiyah, section 1a: top of bed 2 (1).

DESCRIPTION. Tests range from 20 mm to 48 mm in diameter and are circular in outline and bun-shaped in profile. Test height is 39–52% of test diameter (Fig. 12) and in profile the ambitus lies about one third the height above the base.

The apical disc is dicyclic, though occasionally one of the posterior oculars may just be exsert. The apical disc occupies 17–24% of the test diameter (mean = 21%, SD = 1·9%, N = 10; Fig. 12). Genital plates are broad and crescentic in outline, except for the madreporite, which is larger and more pentagonal in outline (Pl. 3, fig. 7; Fig. 13A). Madrepores occupy almost the entire surface of the madreporite plate and

there are small scattered tubercles amongst the openings. Gonopores are present even in the 20 mm diameter individual. Ocular plates are small and pentagonal. All plates have small secondary tubercles, those on the genital plates tending to form a circle around the periproct. The periproct is irregularly oval in outline and occupies 10–14% of the test diameter.

Ambulacra are 17–21% of the test diameter in width at the ambitus (mean = 20%, SD = 1·3%, N = 11). Plating is trigeminate throughout and pore-pairs are arranged either
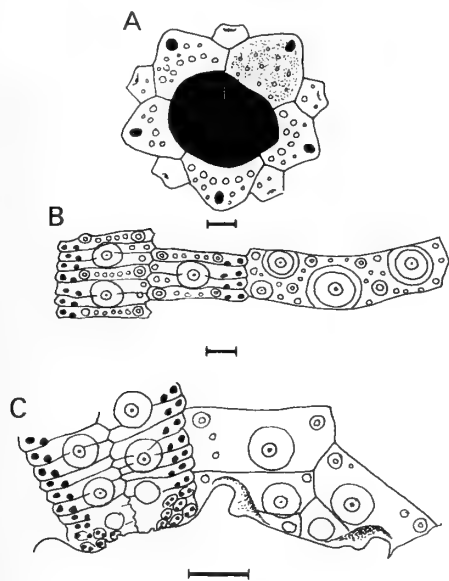
Fig. 13 Camera lucida drawings of plating in *Orthopsis miliaris* (d'Archiac). **A,** apical disc plating, BMNH EE3723; **B,** ambital ambulacral (left) and interambulacral (right) plates, BMNH EE3723; **C,** adoral plating, ambulacrum to left, interambulacrum to right, BMNH EE3733. Scale bars: A, B = 1 mm; C = 2 mm.
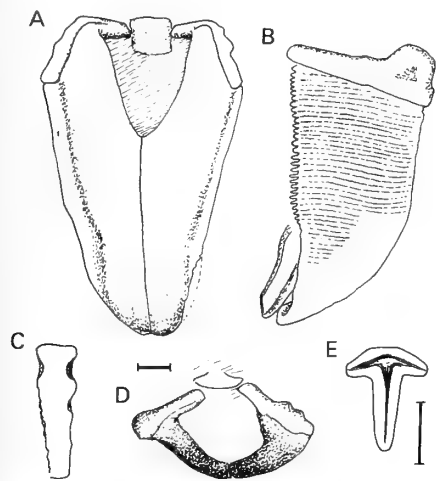
Fig. 14 Camera lucida drawings of lantern elements in *Orthopsis miliaris* (d'Archiac): A-D, BMNH EE3735; E, BMNH EE5020. **A,** pyramid with rotula and tooth in position; **B,** same in lateral view; **C,** fragment of compass element; **D,** adapical view of pyramid, with proximal end of tooth (broken) towards the top; **E,** cross-section of a single tooth. Scale bars = 1 mm.

uniserially or in very weak arcs of three (Pl. 3, fig. 6). All ambulacral elements are narrow and elongate and reach the perradius (Fig. 13B). A primary tubercle (perforate and non-crenulate) straddles two of the three elements in each compound plate (Pl. 3, fig. 6). The third element carries two small secondary tubercles and an intermediate row of miliary granules. There are secondary and miliary tubercles down the perradius also. Adorally only the first five or so pore-pairs are offset to form a weak phyllode (Fig. 13C). There are 55 pore-pairs in a column at 20 mm test diameter, rising to around 90 at 46-48 mm diameter (Fig. 12). Sphaeridial pits are very shallow and are present on the two or three most adoral compound plates, immediately adjacent (perradial) to the pore-pair on the element in each triad that does not support a primary tubercle.

Interambulacra are 38–44% of the test diameter in width at the ambitus (mean = 41%, SD = 2·0%, N = 11) (Fig. 12). Ambital plates are short and wide and slightly curved. At the ambitus most specimens have a single primary tubercle, centrally positioned, plus two smaller secondary tubercles one on either side (Pl. 3, figs 3, 8; Fig. 13B). However, in a fragment of a large specimen (*ca.* 65 mm diameter, BMNH EE3717), there is a fourth large tubercle on the interradial margin. The remainder of the plate carries scattered tertiary tubercles and granules. All tubercles are perforate and non-crenulate. Adorally there is no primordial plate. There are 14 plates in a column at 20 mm test diameter, rising to 18 at 42–48 mm test diameter (Fig. 12).

The peristome is 36–40% of the test diameter in diameter (mean = 38%, SD = 1·7%, N = 7). It is slightly invaginated. There are strong buccal notches that extend into the second interambulacral plate (Pl. 3, fig. 9; Fig. 13C).

The perignathic girdle is seen in BMNH EE3733. The auricles are well developed. They meet and are fused above the perradius to form a continuous arch.

Lantern elements are preserved within the tests of several specimens, but are best seen in BMNH EE3735. Hemipyramids are tall and have a relatively shallow foramen magnum, only some 33% of their height (Figs 14A, B). There is a clear muscle attachment flange on the outer edge of each. The upper surface of the lantern is also pitted. There are well-developed processus superalveolares that extend to the tooth. The lateral (inter-pyramidal) face is denticulate along its inner edge and has the usual horizontal series of ridges for muscle attachment.

The epiphyses are not clearly seen in any specimen but appear relatively short. They are definitely not extended above the foramen magnum nor are they fused together as is the case in camarodont lanterns. There is a single compass element that is slender and has a small head (Fig. 14C). The tooth is strongly keeled and is best seen in cross section in BMNH EE5020 (Fig. 14E).

Spines are seen associated with lantern elements in BMNH EE3735. They are relatively short and needle-like, with a small base and no cortex. The spines are solid, not hollow.

REMARKS. The lantern of *Orthopsis* was described from late Cretaceous specimens of *O. sanfilippoi* Checchia-Rispoli (here treated as a synonym) by Serra (1934), who gave only a sketchy illustration of the apparatus, but pointed out its keeled teeth. Serra, and later Mortensen (1943: 11) described the latern as camarodont. However, this is clearly not the case since the epiphyses are not fused together to form a brace for the tooth. Instead both the hemipyramid and the
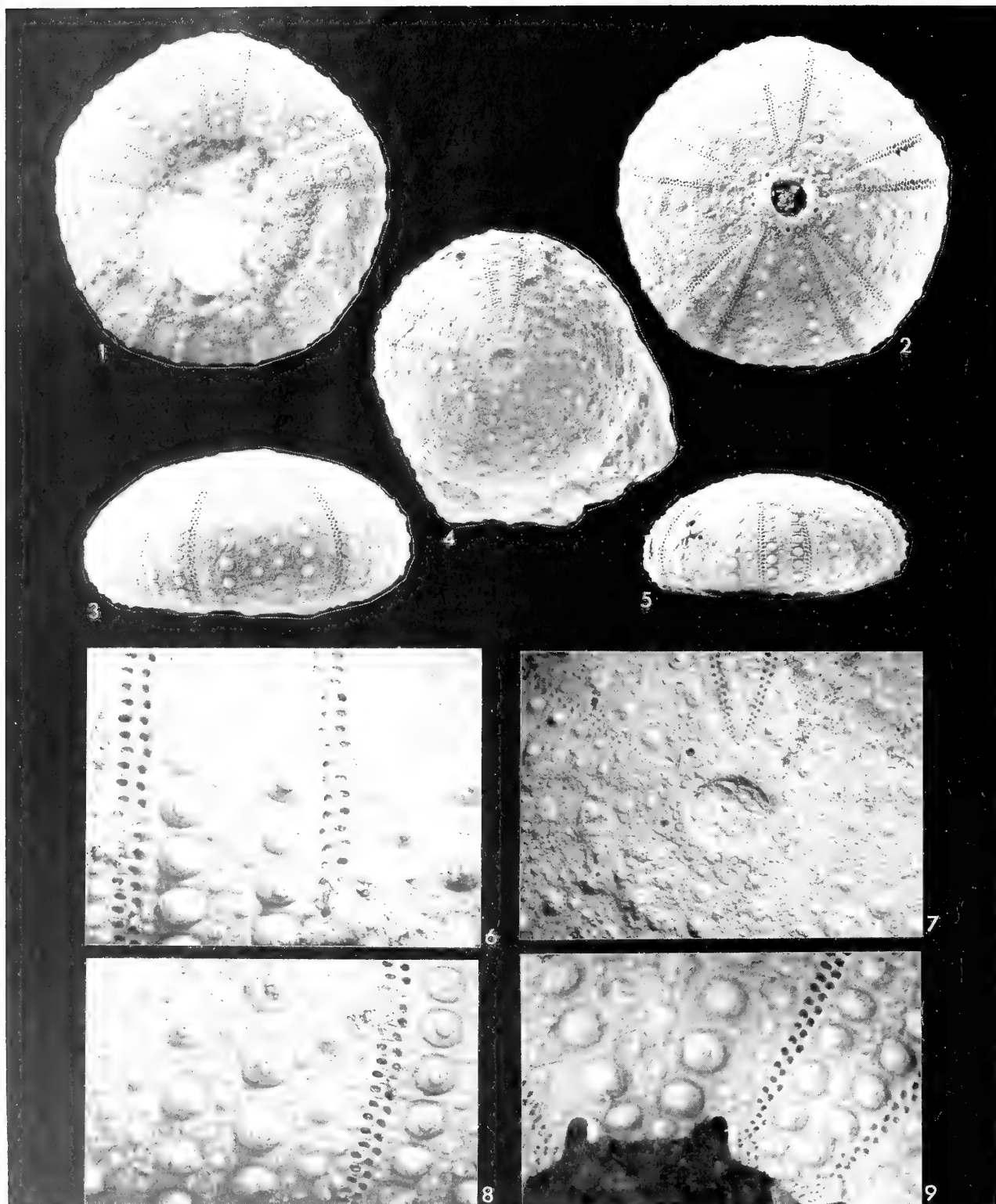
epiphysis extend adaxially towards the tooth as in diadematoid and stirodont lanterns (Jensen 1981, figs 31, 32). The epiphyses are well-separated and although they may actually reach the tooth and support it, they remain far apart. The tooth is undoubtedly keeled and similar to those of stirodonts and camarodonts.

The phylogenetic position of orthopsids can now be clarified. The structure of their epiphyses and hemipyramids is primitive for euechinoids as a whole, thus there are no grounds for treating orthopsids as camarodonts. The keeled teeth and solid spines place orthopsids as acroechinoids and more derived than either diadematoids or echinothurioids. However, the simple acrosaleniid-style of ambulacral plate compounding and the perforate, non-crenulate nature of the primary tubercles differentiate it from all other acroechinoids. They are best considered as an early plesion of the Acroechinoidea.

Orthopsis morgani Cotteau & Gauthier (1895), from the late Senonian of southern Iran (Pl. 2, figs 4, 5) is treated as a synonym.

Order **CALYCINA** Gregory, 1900
Family **SALENIIDAE** Agassiz, 1838
Genus *SALENIA* Gray, 1835

Salenia nutrix Peron & Gauthier, 1881 Pl. 4, figs 1–13;
Pl. 17, figs 4, 5; Figs 15, 16A–E, G, H

1881 *Salenia nutrix* Peron & Gauthier, in Cotteau, Peron & Gauthier: 167, pl. 18, figs 4–10.
1895 *Salenia cossiaea* Cotteau & Gauthier: 83, pl. 13, figs 13–19.
1902 *Salenia cossiaea* Cotteau & Gauthier; Gauthier: 149, pl. 18, fig. 12.
1928 *Salenia cossiaea* Cotteau & Gauthier; Lees: 659.
1932 *Salenia lamberti* Checchia-Rispoli: 6, pl. 2, figs 1–5.
1969 *Salenia geometrica* Agassiz; Devries: 167, pl. 1, fig. 1, pl. 4, figs 1–3.
1989 *Salenia cossiaea* Cotteau & Gauthier; Ali: 398, fig. 2.6.

MATERIAL. 34 specimens, BMNH EE3622–EE3654, EE3656.

OCCURRENCE. In the western Oman Mountian sections studied this species was found as follows:
Jebel Aqabah; lowest few metres of the Simsima Formation (2).
Jebel Buhays, section 1; loose in scree derived from lowest few metres of the Simsima Formation (7).
Jebel Buhays, section 3: loose in scree (2).
Jebel Faiyah, section 1: bed 8 (2).
Jebel Rawdah, section 1; beds 3 and 4 (4); loose in scree (1).
Jebel Rawdah, section 2; beds 6–8 (10); bed 11 (2); bed 13 (2); loose in scree (3).
Jebel Rawdah section 3; bed 2b (1); bed 10 (1).
Jebel Rawdah section 4; bed 10 (1).

This species also occurs in the Upper Campanian of Nafun, 3·5 km west of Surayr, near Dumq, Oman (Skelton *et al.* 1990). It was originally described from the 'Etage dordonien inferieur, couches a *Heterolampas maresi*' (Late Campanian or early Maastrichtian) of Algeria. Later Gauthier (1902) described the same species from the Campanian of Tunisia. Cotteau & Gauthier described a very similar form from the

Senonian of Persia (Iran) under the name *Salenia cossiaea* (Pl. 4, figs 4–6). Finally, Devries (1967) described this species from Turkey under the name *Salenia geometrica* Agassiz.

DIAGNOSIS. Rather inflated species of *Salenia* with seven to eight interambulacral plates at test diameters of 23–28 mm. Apical disc relatively small, circular and flat with periproct and suranal equal in size. Ocular I insert or exsert. Numerous small pits developed along all apical disc sutures in larger specimens, but largest along genital/ocular plate boundaries. Interradial granular zone well developed in specimens greater than 23 mm test diameter.

DESCRIPTION. Tests range in diameter from 7 to 26 mm. Test height in specimens larger than about 10 mm is 60–76% of the diameter (mean 65%, N = 19; Fig. 15). The test is thus rather inflated in profile and in some specimens almost subglobular (Pl. 4, fig. 3).

The apical disc is rather flat and only rises very slightly towards the apex. Its diameter is 42–55% of the test diameter (mean = 46%, N = 19). It is subcircular in outline. The suranal plate is relatively large, on average about 25% of the apical disc diameter. It is similar in size to the genital plates. The periproct is approximately the same size as the suranal plate, or very slightly larger, being on average 27% of the apical disc diameter. In some specimens ocular 1 is strongly exsert and forms the posterior wall of the periproct, but in other specimens ocular 1 is insert and separated from the periproct (Figs 16A-E). Approximately half of the specimens have the ocular plate insert. There is a slight elevation towards the periproct edge, but no true rim is developed. All plates are smooth and unornamented. The sutures are usually incised and may have a series of small pits along their length (Pl. 4, figs 1, 4, 7, 11). The ocular/genital plate boundaries always have pits that are more prominent than the rest. Gonopores are present on genital plates from approximately 10 mm diameter.

Ambulacra are narrow and only very slightly sinuous towards the apex (Pl. 4, fig. 13). They expand adorally to form a short phyllode. Plating is strictly bigeminate throughout. There are 45 pore-pairs in a column at 13 mm test diameter, rising to 78 at 26 mm test diameter (Fig. 15). Each compound plate has a primary tubercle that forms a contiguous row adjacent to the pore-pairs (Figs 16G, H). The perradial zone is narrow, but there is a single secondary tubercle on each compound plate and a single zig-zag row of miliaries also. On the oral surface up to 12 pore-pairs become crowded into a short phyllode in the largest specimens. There are approximately 15 or 16 ambulacral plates opposite an ambital interambulacral plate in individuals of 20–26 mm test diameter.

Interambulacra remain relatively broad throughout. There are six interambulacral plates in a column from 10–16 mm test diameter, rising to eight by about 25 mm diameter (Fig. 15). Plates at the ambitus are slightly wider than tall and the primary tubercle lies towards the adradial margin, leaving a relatively broad interradial zone in specimens larger than about 22 mm diameter. Primary tubercles are imperforate and crenulate and are surrounded by five or six secondary tubercles (non-contiguous) (Pl. 4, fig. 13). The interradial zone has miliary tubercles from about 15 mm test diameter upwards and in larger specimens this forms a broad and distinctive band that runs almost to the peristome edge.

The peristome is on average 48% of the test diameter
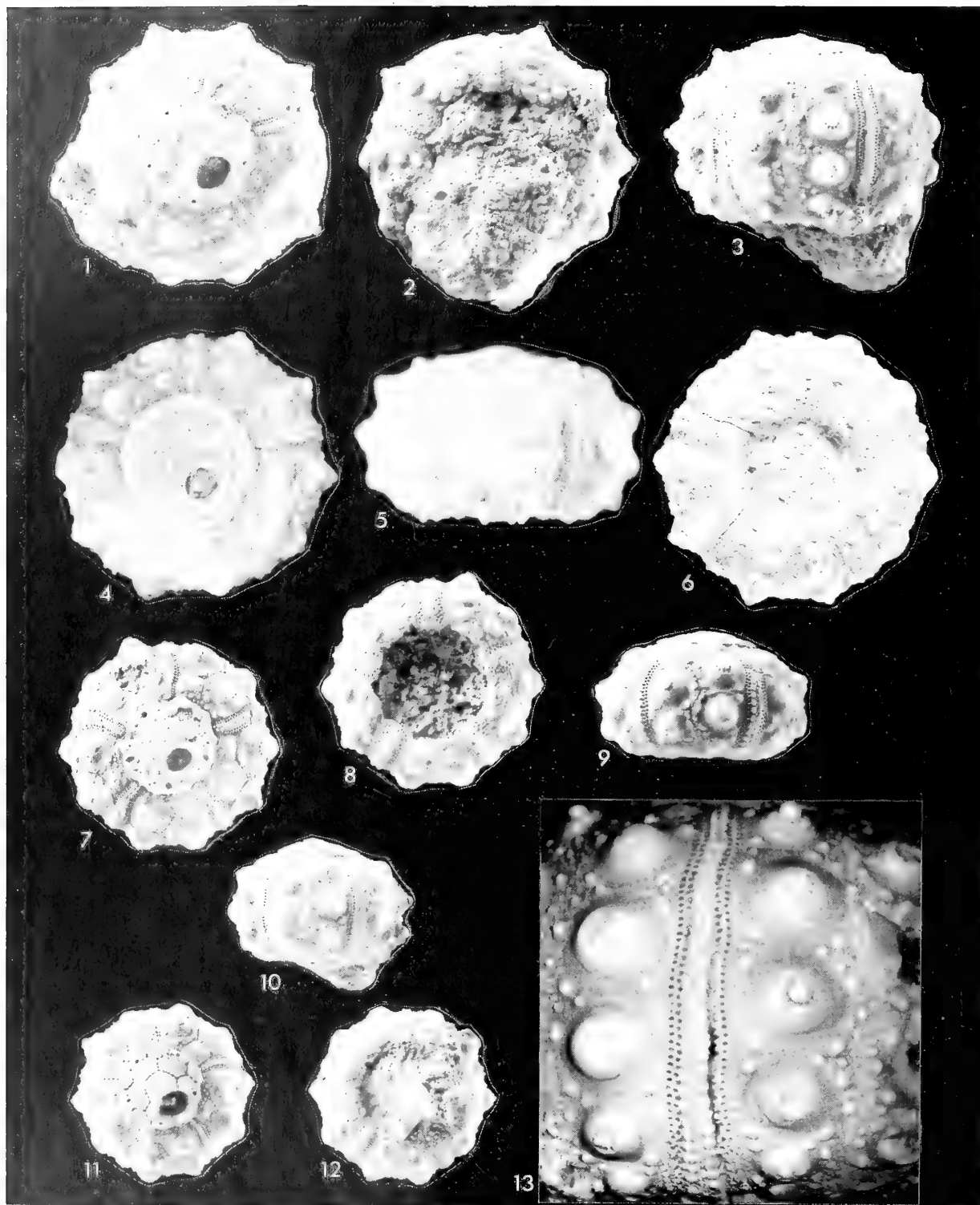
PLATE 4

Figs 1–13 *Salenia nutrix* Peron & Gauthier. **1–3, 13**, BMNH EE3646; **1**, apical, × 2; **2**, oral, × 2; **3**, lateral, × 2; **13**, ambital detail, × 5. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation. **4–6**, B18723a, Museum d'Histoire Naturelle, Paris; topotype material from the Morgan Collection of *Salenia cossiae* Cotteau & Gauthier; **4**, apical; **5**, lateral; **6**, oral; all × 3. Senonian, Kala é Melek, Iran. **7–9**, BMNH EE3651; **7**, apical; **8**, oral; **9**, lateral; all × 2. Jebel Buhays, lowest 2 m of the Simsima Formation. **10–12**, BMNH EE3652; **10**, lateral; **11**, apical; **12**, oral; all × 2. Jebel Buhays, lowest 2 m of the Simsima Formation.
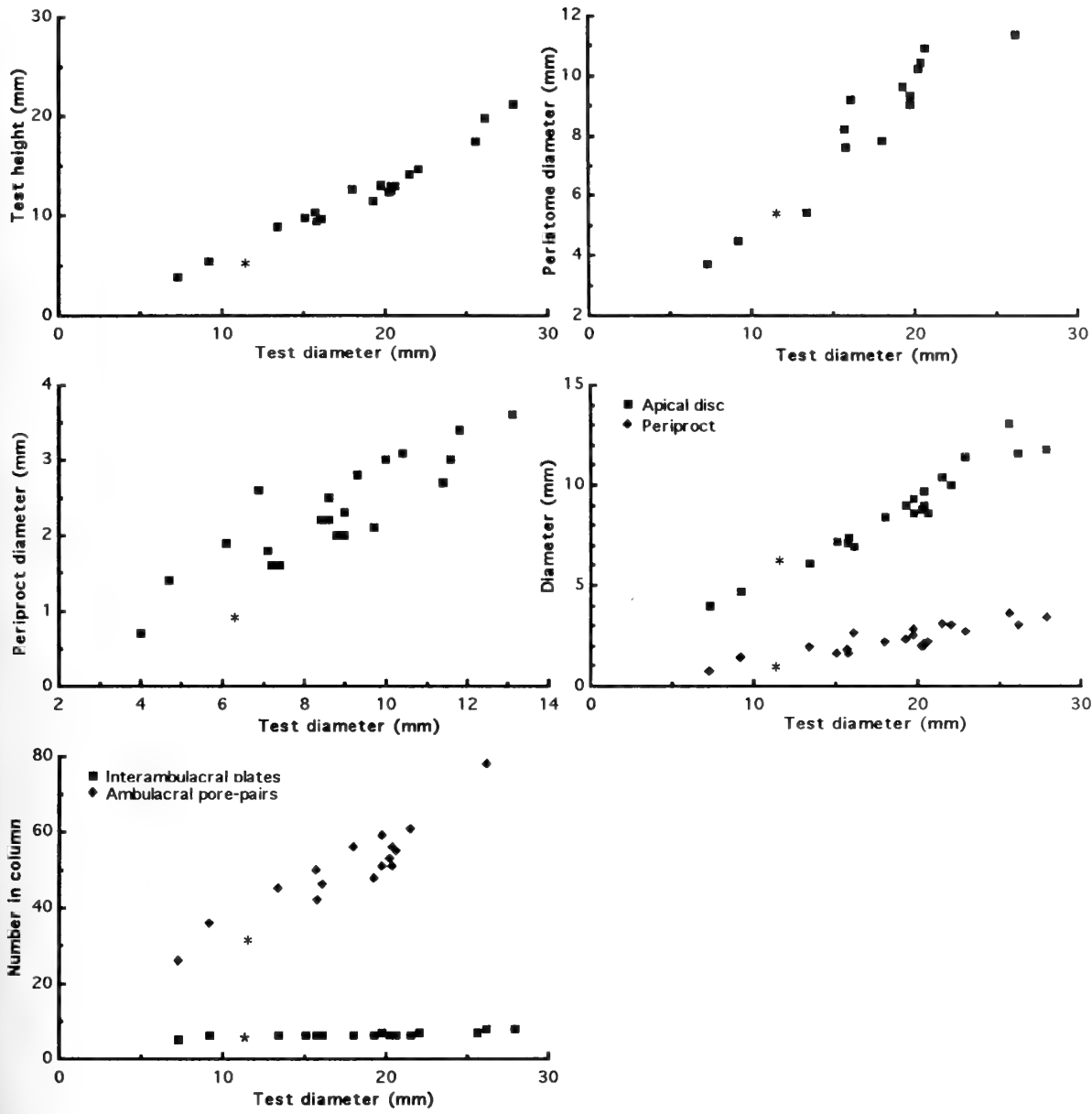
Fig. 15 Biometric data for *Salenia nutrix* Peron & Gauthier (squares) and *S. microprocta* sp. nov. (crosses).

across. It is hardly invaginated and has feeble buccal notches (Pl. 4, figs 2, 6, 8, 12).

REMARKS. This species somewhat resembles *S. geometrica* Agassiz, but differs from that species in having a relatively smaller apical disc and a larger periproctal opening. It also has much less pronounced pits developed at triple suture junctions on the apical disc. Although there are clearly two morphological forms, those with ocular 1 insert and those with ocular 1 exsert, the apical discs are in all other respects identical and the two forms co-occur in the various sections. I therefore treat the two forms as variants of the same species. The form described by Checchia-Rispoli (1932a) as *S. lamberti* from the Maastrichtian of Libya has all the characteristics of *S. nutrix*, except that ocular 1 is reportedly always

insert. It too is treated as part of this same species complex. *S. nutrix* resembles *S. loveni* (Cotteau) in having a rather flat and smooth apical disc and in having expanded phyllodes adorally. However, it is very different both in the relative size of the apical disc (which in *S. loveni* occupies most of the upper surface) and in the coarseness of the tuberculation. *S. maxima* Arnaud and *S. belgica* Lambert are also similar in having fine sutural pitting but also have relatively much larger apical discs than is seen in *S. nutrix*.
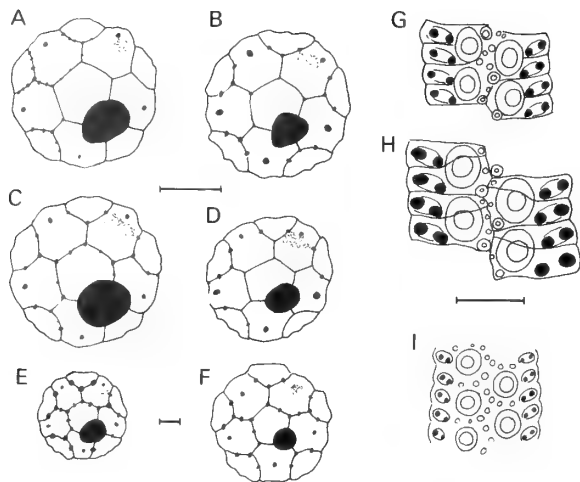
Fig. 16 Camera lucida drawings of plating in *Salenia*. **A-E**, apical discs of *Salenia nutrix* Peron & Gauthier; A, BMNH EE3646; B, BMNH EE3654; C, BMNH EE3647; D, BMNH EE3651; E, BMNH EE3627. **F**, apical disc of *Salenia microprocta* sp. nov. BMNH EE3657. **G, H** ambital ambulacral plating of *Salenia nutrix* Peron & Gauthier; G, BMNH EE3647; H, BMNH EE3638. **I**, ambital ambulacral plating of *Salenia microprocta* sp. nov., BMNH EE3657. Scale bars; A-D = 5 mm; E, F = 1 mm; G-I = 1 mm.

Salenia microprocta sp. nov   Pl. 5, figs 13; Figs 15, 16F, I

TYPE. Holotype and only known specimen, BMNH EE3657.

OCCURRENCE. Jebel Huwayyah, section 2: bed 1.

DIAGNOSIS. A small, flattish *Salenia* with a relatively large, flat, pentagonal apical disc and a small oval periproct. Ambulacral tubercles are not contiguous and at the ambitus may be separated by granules.

DESCRIPTION. Test 11·4 mm in diameter and 5·1 mm in height (45% of test diameter). Depressed in profile with a broad flat base and top. The ambitus is uniformly rounded. The apical disc is flat and pentagonal in outline, with the angles radial. The disc is 55% of the test diameter in length. The genital plates are approximately as broad as long and are all similar in size (Fig. 16F). Ocular plates protrude slightly. The suranal plate is relatively large, whereas the periproct is small (Pl. 5, fig. 1), being only 17% of the apical disc diameter along the plane of bilateral symmetry. There is no lip to the periproct. Sutural pits are present at all plate triple junctions and also mid-way between these junctions. Small gonopores are present.

The ambulacra are slightly sinuous adapically, becoming straight adorally and expanding towards the peristome. There are 33 pore-pairs in a column and 16 primary tubercles. All plates are compound and bigeminate. At the ambitus the ambulacral width is 1·5 mm with the perradial tuberculate zone making up 1·0 mm of this width. Primary tubercles are relatively small and are not contiguous with their neighbours. There is a single row of miliary tubercles perradially and, at the ambitus, there is also a single row of miliaries between successive primary tubercles (Pl. 5, fig. 3; Fig. 16I). Small phyllodes are developed adorally.

Interambulacra are composed of five plates in each column. Each has a single primary tubercle surrounded by six widely-spaced scrobicular tubercles. There is a single row of miliary tubercles down the interradius.

The peristome is very slightly invaginated and is 50% of the test diameter in diameter. There are feeble buccal notches.

REMARKS. No other *Salenia* species has ambulacra with primary tubercles separated by rows of granules. *S. microprocta* is also easily distinguished from small specimens of *S. nutrix* by the very small size of its periproct and the relatively large area occupied by the apical disc.

Order **ARBACIOIDA** Gregory, 1900
Family **GONIOPYGIDAE** Smith & Wright, 1993
Genus ***GONIOPYGUS*** Agassiz, 1838

Goniopygus arabicus sp. nov. Pl. 6, figs 3–10; Pl. 7, figs 1, 3, 5, 6; Figs 17, 18A, B, D, E, G

1972   *Goniopygus superbus* Cotteau & Gauthier; Kier: 68, pl. 42, figs 1–3.
1989   *Goniopygus superbus* Cotteau & Gauthier; Ali: 401, fig. 2 (2).

TYPES. The holotype is BMNH EE4012, paratypes are BMNH EE3983–84, EE39896, EE3992, EE3997, EE4005, EE4007, EE4015, EE4017 and EE4019.

MATERIAL STUDIED. Forty-four specimens of which the type series was used in the biometric analysis.

OCCURRENCE. In the western Oman Mountains this species is found at the following levels:
Jebel Buhays, section 1: loose in scree derived from the lowest few metres of the Simsima Formation (29): bed 12 (1).
Jebel Buhays, section 2: loose in scree derived from the basal few metres of the Simsima Formation (4).
Jebel Buhays, section 3: basal 1 m of the Simsima Formation (4).
Jebel Thanais: lowest 1 m of the Simsima Formation (2).
Jebel Faiyah, section 1: bed 6 (1 fragment).
Jebel Rawdah, section 2: bed 4 (1): beds 6–8 (10); bed 10 (1); bed 11 (1).
Jebel Rawdah, section 3a, bed 2 (2).

Elsewhere the species has been reported from the late Campanian of the Rihyad district of Saudi Arabia (Kier 1972).

DIAGNOSIS. A species of *Goniopygus* with relatively narrow ambulacra with a single small secondary tubercle on each compound plate, a trigonal periproct with, predominantly, three perianal tubercles and apical disc plating that is smooth and unornamented. Gonopores lie on the genital plates.

DESCRIPTION. Tests range in size from 25 to 41 mm in diameter and are circular in outline. Test height is 53–62% of test diameter (mean = 57%, SD = 3·0%, N = 9: Fig. 17). Both the base and top are flat in profile and the ambitus lies at approximately mid-height (Pl. 6, figs 4, 5, 7). The apical disc plates are elevated above the corona.

The apical disc is flat, large and prominent. It occupies 35-43% of the test diameter (mean = 40%, SD = 3·3%, N = 9). Genital plates are pointed distally and the gonopore opens
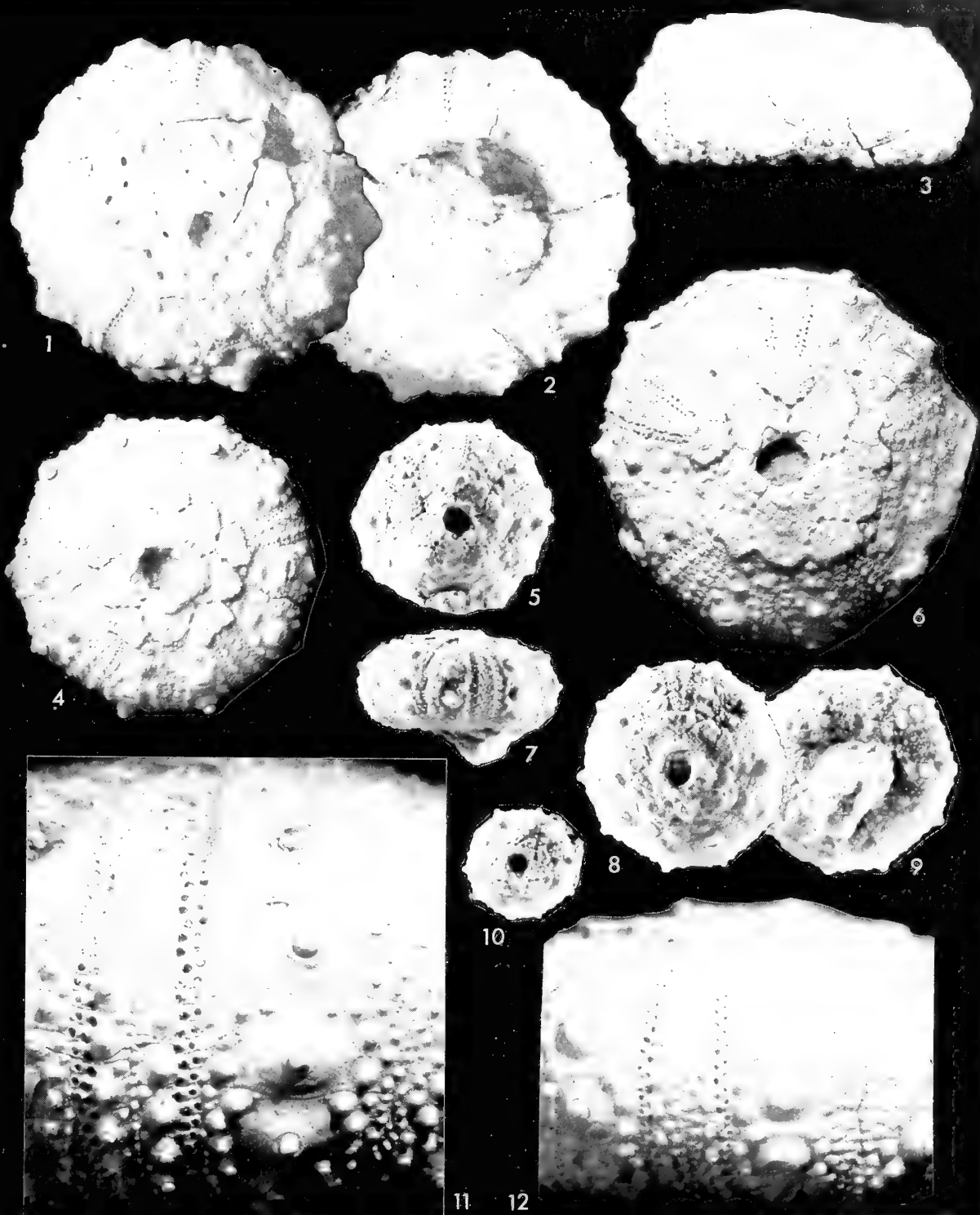
PLATE 5

Figs 1–3 *Salenia microprocta* sp. nov. BMNH EE3657, holotype; **1**, apical; **2**, oral; **3**, lateral; all × 6. Jebel Huwayyah, section 2, bed 1.

Figs 4–10, 12 *Mimiosalenia quinquetuberculata* gen. et sp. nov. Jebel Faiyah, section 1, bed 7. **4, 12,** BMNH EE3981, holotype; **4**, apical, × 4; **12**, lateral, ambulacrum detail, × 8. **5, 6,** BMNH EE3982, paratype, apical; **5**, × 3; **6**, × 6. **7–9,** BMNH EE3978, paratype; **7**, lateral; **8**, apical; **9**, oral; all × 3. **10,** BMNH EE3980, paratype; apical, × 3.

Fig. 11 *Glyphopneustes hattaensis* Ali. BMNH EE4027, detail of ambital region, lateral view, × 8; Jebel Thanais, lowest 2 m of the Simsima Formation.

Fig. 17 Biometric data for *Goniopygus arabicus* sp. nov.

beyond the tip of the apical disc platform, though still within the genital plate (Figs 18A, B). Ocular plates are relatively large and are insert. All plates are flat and smooth, without ornamentation. The periproct is oval and lies slightly posterior of centre. It is approximately 9–12% of the test diameter in width along the anterior-posterior axis. In the great majority of specimens the opening is trigonal and there are three perianal tubercles on genital plates (Pl. 7, fig. 1). However, there is a single specimen (BMNH EE3983) that has five perianal tubercles (Pl. 6, fig. 9) and one that has four, thus the number of tubercles is not invariant.

The ambulacra are 13–14% of the test diameter in width at the ambitus. All plates are compound and trigeminate, with a demiplate and two full elements (Fig. 18D). The two major elements carry a single primary tubercle and the upper also

has a perradial secondary tubercle in addition (Fig. 18E). The perradial tuberculate zone thus is composed of an outer series of primary tubercles alternating with a distinct inner series of secondary tubercles (Pl. 7, fig. 3). All tubercles are imperforate and non-crenulate. Below the ambitus pore-pairs are small and oval and become crowded close to the peristome to form a relatively well-developed phyllode (Pl. 7, fig. 5). At the ambitus pore-pairs become markedly more elongate and the individual pores more widely separated. Individual pores in a pore-pair are distinctly conjugate in larger individuals. There are no sphaeridial pits. There are 56 pore-pairs and 19 primary tubercles in a column at 25 mm test diameter, rising to 77 pore-pairs and 25 primary tubercles at 41 mm test diameter (Fig. 17).

Interambulacra are broad and each plate carries a large
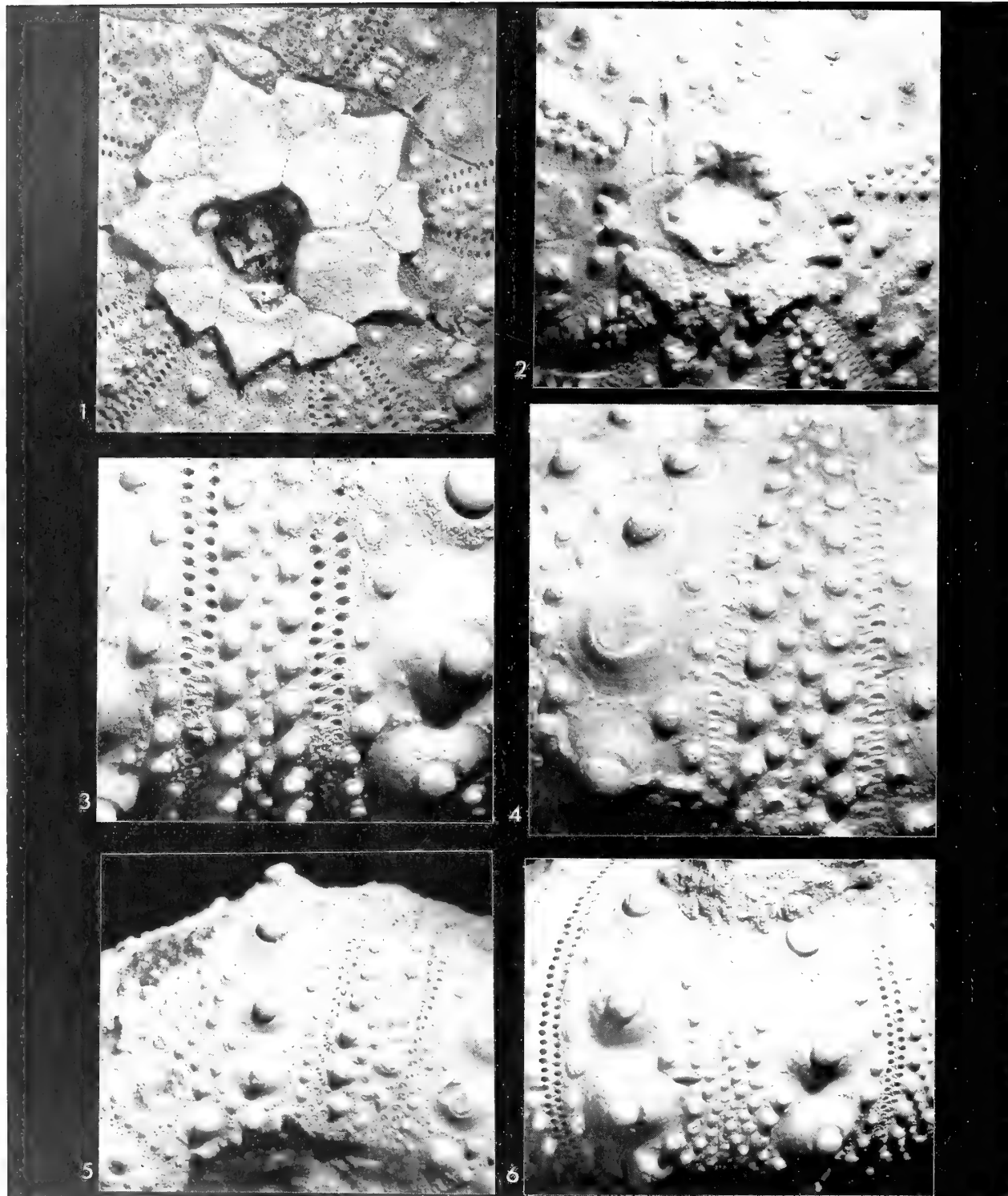
PLATE 7

Figs 1, 3, 5, 6   *Goniopygus arabicus* sp. nov. **1, 2**, BMNH EE4012, holotype; apical disc, × 5. Jebel Rawdah, section 3, bed 2. **3, 6**, BMNH
EE4015, paratype; **3**, detail of ambulacrum at ambitus, × 5; **6**, detail of interambulacrum at ambitus, × 3. Jebel Thanais, lowest 1 m of the
Simsima Formation. **5**, BMNH EE3997, adoral detail, × 3·5. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the
Simsima Formation.

Figs 2, 4   *Goniopygus superbus* Cotteau & Gauthier, L12680, Lambert Collection, Geology Department, Université de Paris VI, Paris; **2**,
apical disc, × 4; **4**, detail of ambulacrum at ambitus, × 6. Derré-i-Chahr, Iran.
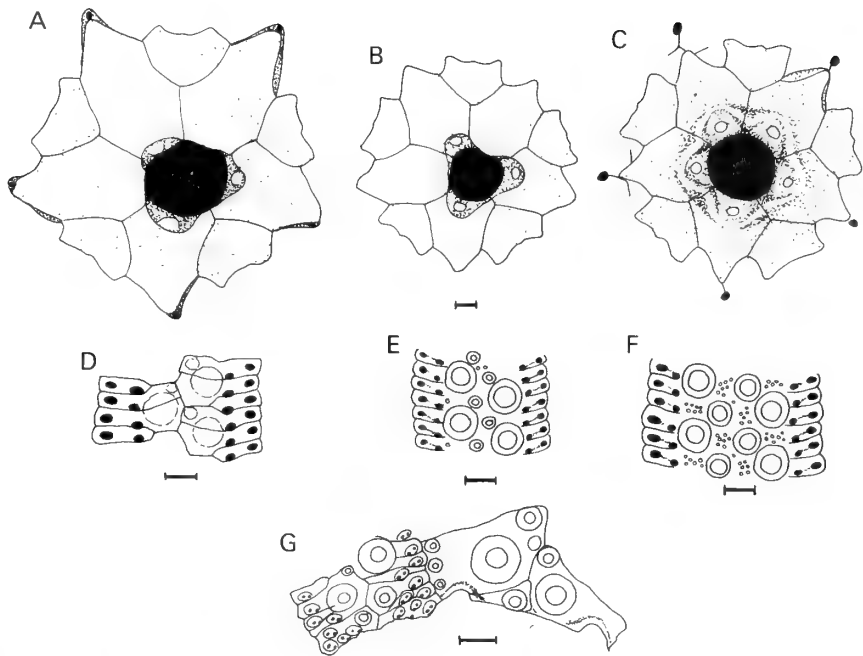
Fig. 18 Camera lucida drawings of *Goniopygus* species. **A, B** apical disc plating of *Goniopygus arabicus* sp. nov.; A, BMNH EE4017; B, BMNH EE4005. **C, F,** apical disc plating and ambital ambulacral tuberculation of *Goniopygus superbus* Cotteau & Gauthier, L12680, Geology Department, Universite de Paris VI; Senonian, Derre-i-Chahr, Iran. **D, E**, ambital ambulacral plating, *Goniopygus arabicus* sp. nov.; D, BMNH EE4017; E, BMNH EE4005. **G**, *G. arabicus* sp. nov., adoral plating, ambulacrum to left, BMNH EE3986. Scale bars = 1 mm.

primary tubercle. At the ambitus interambulacral width is 42–46% of the test diameter. There are 8 plates in a column at 25 mm diameter, rising to 11 at about 40 mm test diameter (Fig. 17). Primary tubercles are stout, imperforate and non-crenulate at the ambitus, but reduce sharply in size adapically so that the top three or four tubercles are very small. At the ambitus they are surrounded by about 6 widely-spaced scrobicular tubercles (Pl. 7, fig. 6). Down the interradius there is a single column of secondary tubercles on each plate. Adorally both columns of plates reach the peristomial margin and there is no primordial plate (Fig. 18G).

The peristome is slightly invaginated and is 37–44% of the test diameter in diameter (mean = 42%, SD = 2·6%, N = 7). Buccal notches are relatively small and poorly differentiated, with only a weak rim.

REMARKS. This species was described under the name *Goniopygus superbus* Cotteau & Gauthier by Kier (1972) and Ali (1989). It differs from that species in several important respects. Firstly, the apical disc of *G. superbus* has a larger periproctal opening and has either five, or rarely four perianal tubercles (Pl. 6, figs 1, 2; Pl. 7, fig. 2; Fig. 18C). These perianal tubercles face upwards and the adjacent portions of the genital plates are raised in the form of a very characteristic stellate rim. The radial portions of this rim project upwards as blunt denticles. Furthermore, the apical disc plates of *G. superbus* are covered in fine granular ornament. The gonopores in all specimens studied open not in the genital plates, but within the interambulacral plates some one or two plates distant from the apical disc (Fig. 18C). Finally, the ambulacral tuberculation affords an easily distinguishable

character: in *G. superbus* the ambulacra are wide and the inner series of secondary tubercles almost as large as the primary tubercles, whereas in *G. arabicus* the ambulacra are narrow and the secondary tubercles very much smaller (compare Pl. 7, fig. 3 and Fig. 18E, with Pl. 7, fig. 4 and Fig. 18F). Finally, in *G. superbus* there are zones of small miliary granules separating successive tubercles which are totally absent in *G. arabicus*.

Genus *MIMIOSALENIA* gen. nov.

TYPE SPECIES. *Mimiosalenia quinquetuberculata* sp. nov.

DIAGNOSIS. A goniopygid with a perianal tubercle on each genital plate and pits along apical disc sutures. Ambulacra bigeminate except adorally where occasional simple plates are intercalated.

OCCURRENCE. Known only from the late Cretaceous (Maastrichtian) of Jebel Faiyah, section 1, western Oman Mountains.

REMARKS. This genus is closely related to *Goniopygus* on account of its distinctive apical disc plating. The five gonopores lie immediately beyond the genital plates and open in the interambulacra. The genital plates of the apical disc have perianal tubercles identical to those of *Goniopygus* and the stellate ridge surrounding them is very reminiscent of that seen in *G. superbus* Cotteau & Gauthier. However, there are well-developed sutural pits both at triple junctions and mid-length along the plate sutures on all apical disc plates, which
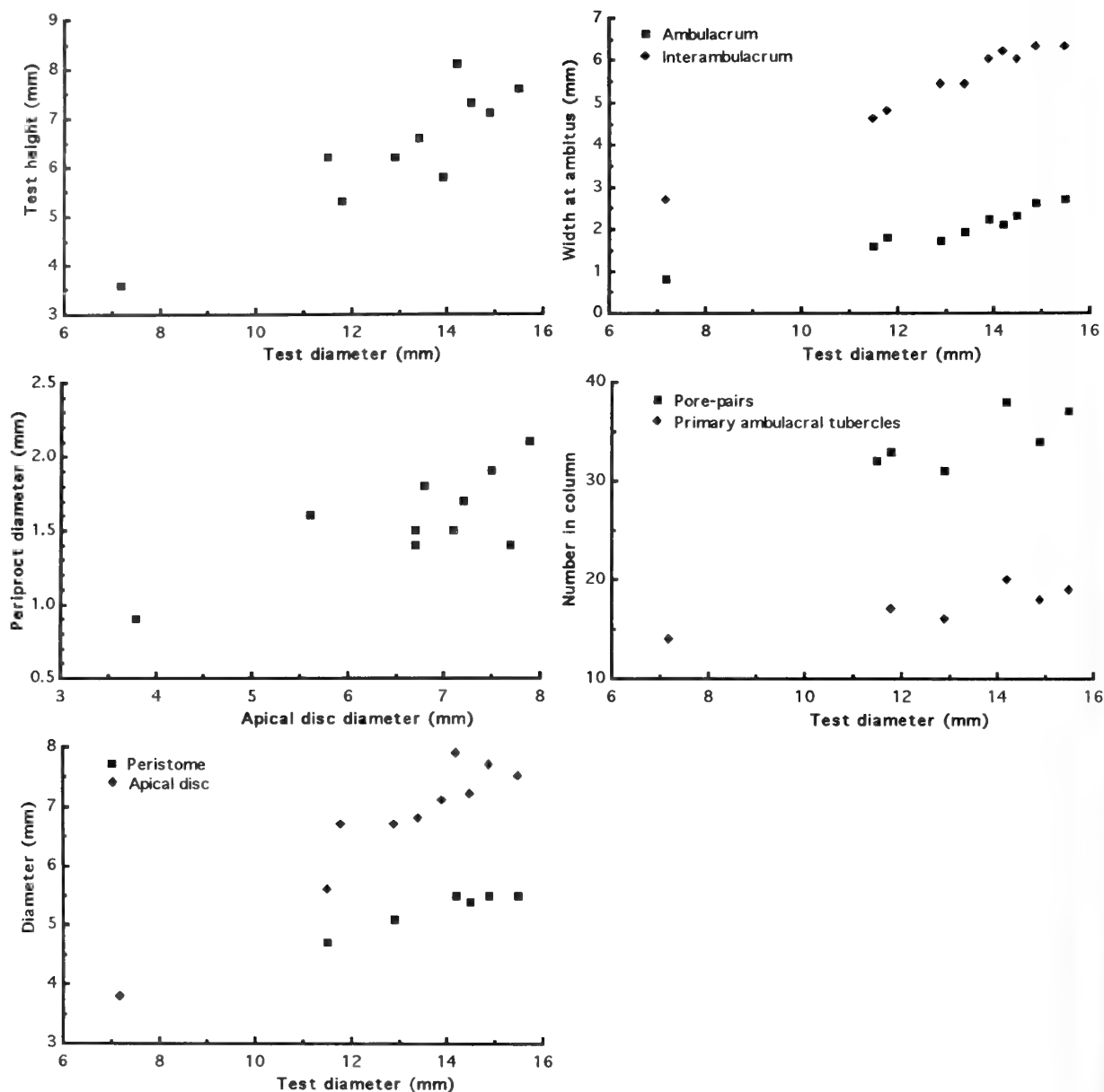
Fig. 19 Biometric data for *Mimiosalenia quinquetuberculata* sp. nov.

are often seen in saleniids but are never seen in *Goniopygus*. Another major difference between *Goniopygus* and *Mimios-alenia* is that the ambulacra of *Goniopygus* are trigeminate or occasionally quadrigeminate, whereas those of *Mimiosalenia* are strictly bigeminate, except close to the peristome where plating tends to become unigeminate. Again, bigeminate plating is typical of saleniids. All ambulacral plates in *Mimi-osalenia* reach the perradius and are approximately equal in size, whereas in *Goniopygus* there is a demiplate and the other two plates in each triad are unequal in size.

Despite the similarities to *Salenia*, *Mimiosalenia* lacks a suranal plate and has the highly characteristic apical disc structure of a goniopygid. For this reason I believe it to be a derived goniopygid that has developed sutural pitting and

bigeminate plating through the loss of the demiplate in each triad.

Mimiosalenia quiquetuberculata sp. nov Pl. 5, figs 4–10, 12; Figs 19, 20

TYPES. Holotype, BMNH EE3981; paratypes, BMNH EE3971, EE3974, EE3977–78, EE3980, EE3982, EE5014–17.

MATERIAL STUDIED. Biometric data is taken from the type series. In addition there are six other specimens.

OCCURRENCE. The species is known only from bed 7, section 1b, Jebel Faiyah, western Oman Mountains.

DIAGNOSIS. As for generic diagnosis: apical disc with five perianal tubercles. Gonopores lie just outside the genital plates in the interambulacral areas.

DESCRIPTION. Tests range from 7·2 to 15·5 mm in diameter and are circular in outline. Test height is 42–57% of test diameter with the flatter tests possibly representing slightly crushed specimens (Fig. 19). In profile the apical disc is very slightly conical and the sides uniformly rounded so that the ambitus lies at about mid-height.

The apical disc is relatively large and raised above the coronal plates (Pl. 5, fig. 7). It is 48–57% of the test diameter across (Fig. 19) with the periproct more or less centrally positioned. Ocular plates are relatively large and square-ended. The five genital plates border the periproct and are bluntly pointed distally (Figs 20A, B). All plates are smooth and unornamented. Each genital plate has a single perianal tubercle adjacent to the periproct. The genital plates are raised to form a stellate rim surrounding these perianal tubercles (Pl. 5, figs 4, 6; Figs 20A, B). All five genital plates are approximately the same size. Gonopores open beyond the genital plates and are found immediately adjacent in the interambulacral zones (Fig. 20B). They are only present in the larger specimens, *ca.* 14 mm diameter. The periproct is subcircular in outline and measures 9–15% of the test diameter in width (Fig. 19).

Ambulacra are relatively broad and slightly concave perradially. They are 11–17% of the test diameter in width at the ambitus. From the apex to below the ambitus plating is strictly bigeminate (Pl. 5, fig. 12; Fig. 20C), with each element reaching the perradius (Fig. 20D). Each pair of elements bears a large primary tubercle. Close to the peristome there are occasional simple elements interspersed, each with a large primary tubercle. There are 31–32 pore-pairs and 16–17 primary tubercles in a column at 11·5–13 mm test diameter, rising to 37 pore-pairs and 19 primary tubercles at 15·5 mm test diameter (Fig. 19). The perradial zone of tuberculation is very broad and contains a mixture of secondary tubercles and granules, two or three abreast (Pl. 5, fig. 12; Fig. 20C). Adorally the pore-pairs are slightly more widely separated and there is no phyllode development whatsoever. Ambulacra hardly taper either adorally or adapically. There are no sphaeridial pits.

Interambulacra are 38–44% of the test diameter in width at the ambitus. There are seven plates in a column at 6·2 mm test diameter, rising to eight or nine at 15 mm test diameter. Each plate carries a large primary tubercle which is non-crenulate and imperforate. The most adapical two are generally very much smaller than the remainder. The primary tubercles have six scrobicular tubercles, three on each side, that are more or less contiguous (Pl. 5, fig. 12). The interradial zone is broad and slightly concave. It is occupied by a series of miliary tubercles, two to each plate (four abreast). There is no primordial plate adorally and both columns reach the peristomial border.

The peristome is circular, slightly invaginated and occupies 6–40% of the test diameter. Buccal notches are small and indistinct (Pl. 5, fig. 9).

Spines, lantern and perignathic girdle all unknown.

REMARKS. The biserial nature of the ambulacra and the characteristic apical disc structure make this species easy to distinguish from any other described here.
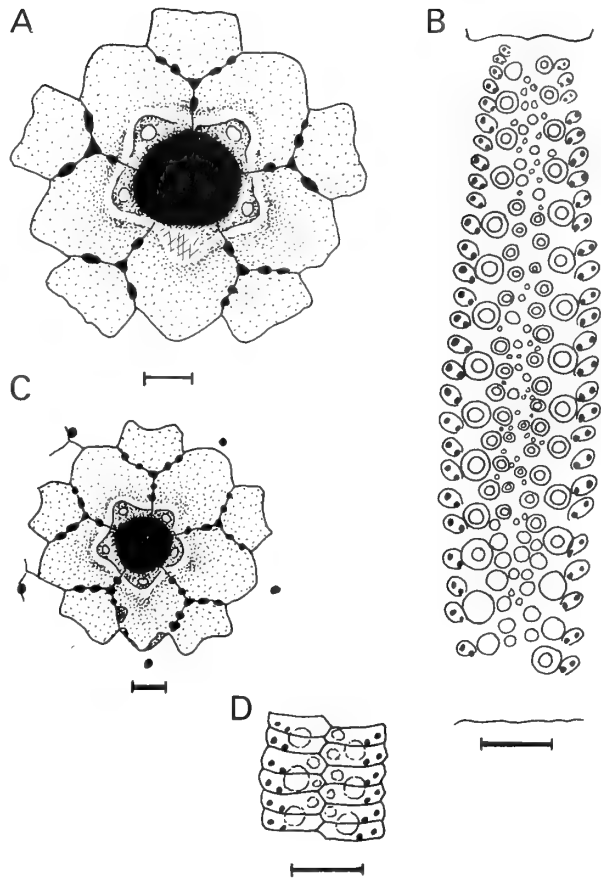
Fig. 20 Camera lucida drawings of plating in *Mimiosalenia quinquetuberculata* sp. nov. **A,** apical disc, BMNH EE3981; **B,** apical disc, BMNH EE3982; **C,** ambulacrum, from apical disc (top) to peristomial margin (bottom), BMNH EE3981; **D,** ambital ambulacral plating, BMNH EE5014–17. Scale bars = 1 mm.

Family **GLYPHOPNEUSTIDAE** Smith & Wright, 1993
Genus *GLYPHOPNEUSTES* Pomel, 1883

Glyphopneustes hattaensis Ali, 1992 Pl. 5, fig. 11; Pl. 8, figs 1–12; Figs 21, 22

1992a *Glyphopneustes hattaensis* Ali: 68, fig. 3.

TYPES. Holotype, the figured specimen, housed in the Geological Museum, University of Al Ain, United Arab Emirates.

MATERIAL STUDIED. 82 specimens, of which biometric data was taken from the following 30: BMNH EE3909, EE3913, EE3915, EE3919–20, EE3923–24, EE3926, EE3930–31, EE3934, EE3936–38, EE3940, EE3942–43, EE3945–47, EE3949, EE3953–54, EE3958, EE3960, EE3967–70.

OCCURRENCE. The type material all comes from Jebel Rawdah. This species was collected at the following levels:
Jebel Huwayyah, section 2: bed 1 (1).
Jebel Faiyah, section 1: bed 2 (1); bed 5 at base (1); bed 8 (9); loose approximately 10 m above base of the Simsima Formation (1).

Jebel Buhays section 1; loose, derived from lowest few metres of the Simsima Formation (50).

Jebel Thanais; lowest 2 m of the Simsima Formation (6).

Jebel Rawdah, section 1; bed 4 (1).

Jebel Rawdah, section 2; beds 9/10 (2); bed 11 (5); bed 13 (1); loose (6).

Jebel Rawdah, section 3; bed 2 (2); bed 5 (1).

Jebel Rawdah, section 4; bed 4 (1).

DESCRIPTION. Tests range in diameter from 10 to 30 mm, with the great majority around 18–24 mm diameter (Fig. 21). The test is circular in outline and depressed in profile, with a rounded ambitus, although some specimens are slightly more conical. Test height is 39–57% of the diameter (mean = 50%,

SD = 4·0%, N = 30; Fig. 21). The ambitus lies at about mid-height.

The apical disc is highly sculpted and occupies 25–42% of the disc diameter (mean = 32%, SD = 1·2%, N = 30). It is proportionally larger in small individuals (Fig. 21). The periproct is large and central, occupying 30–50% of the apical disc diameter (mean = 40%, SD = 4·9%, N = 28). It is oval in outline with smoothly rounded edges (Pl. 8, figs 1, 2). The apical disc is dicyclic and all five genital plates are approximately equal-sized (Fig. 22B). There is a rim surrounding the periproct which bears a large central tubercle and two lateral tubercles. The gonopores open at the outer edge of the genital plates. The madreporite has a horse-shoe-shaped zone of madrepores that open around its margin (Fig. 22B).
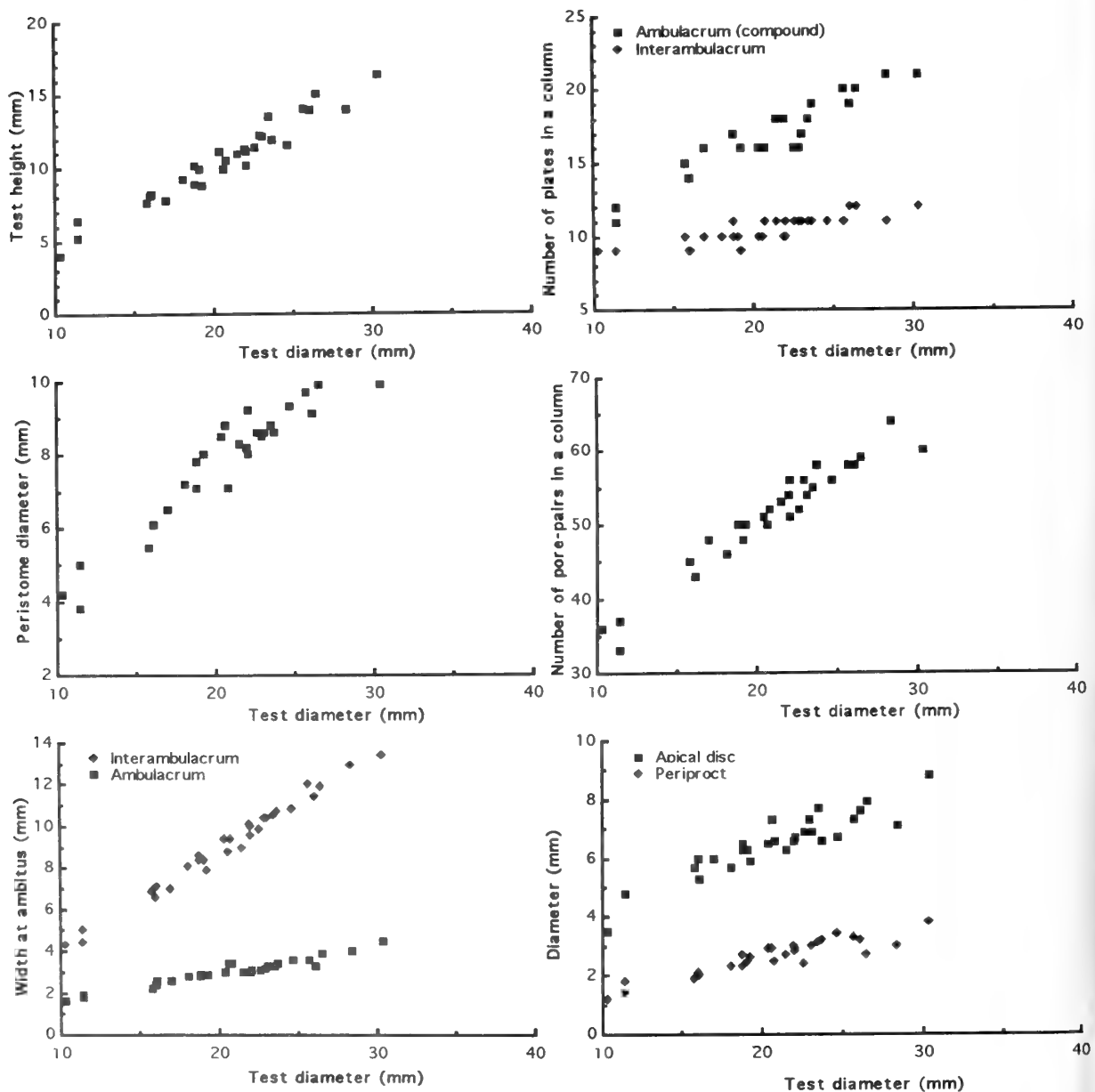
Fig. 21 Biometric data for *Glyphopneustes hattaensis* Ali.

Ocular plates are heart-shaped. The sutures are all deeply incised and there are typically three small tubercles along the ocular/genital plate boundary within these depressed regions.

Ambulacra are 13–17% of the test diameter in width at the ambitus (Fig. 21). All plates are trigeminate and there is a single demiplate in each triad (Figs 22A, C). The two full elements bear a single large primary tubercle that is imperforate and non-crenulate. The upper element is smaller than the lower. Towards the peristome the demiplate has a shallow pit immediately perradial to the pore-pair, which marks the site of a sphaeridium (Pl. 8, fig. 3; Fig. 22D). There are four or five of these in each column. Pore-pairs are uniserially arranged and not noticeably enlarged ambitally and adapically. There is no pore crowding whatsoever close to the peristome. There are around 33 pore pairs and 11 primary tubercles in a column at 11 mm test diameter, rising to about 60 pore-pairs and 21 primary tubercles (Fig. 21). There is a single row of scattered miliary tubercles down the perradius.

Interambulacra are 39–46% of the test diameter in width at the ambitus (mean = 44%, SD = 1·8%, N = 30). There are 9 plates in a column at 10 mm test diameter, rising to 12 at 30 mm test diameter (Fig. 21). Ambital plates are much wider than tall and each bears a single large primary tubercle that is non-crenulate and imperforate (Pl. 8, fig. 6). The most adapical two or three plates have significantly smaller tubercles than the rest. The primary tubercles have three scrobicular tubercles on either side, but have confluent areoles within each column. Down the interradius there are two or three irregular rows of scattered secondary and miliary tubercles, forming a relatively broad granular zone (Pl. 8, fig. 6). Adorally both columns of plates reach the peristome and there is no primordial plate.

The peristome is rather small and not at all invaginated. It is 33–43% of the test diameter across (mean = 38%, SD = 2·9%, N = 27), proportionally smaller in larger individuals (Fig. 21). Buccal notches are relatively shallow.

REMARKS. Ali (1992a) gave a detailed description of this species but based on only six specimens. The large number of well-preserved specimens now to hand allows a detailed biometric description of this species for the first time. Ali specifically stated that sphaeridial pits were lacking in this species, yet in well-preserved specimens such pits can be seen. The difference between this species and the Cenomanian G. problematicus rest almost entirely on the apical disc ornamentation and the absence of sutural pits on the interambulacral plates of G. hattaensis. Although Fell & Pawson (1966) placed Glyphopneustes in the family Hyposaleniidae, and were followed by Smith & Wright (1990), it is now evident from the material available that Glyphopneustes is an arbacioid, and has been placed in its own family Glyphopneustidae by Smith & Wright (1993). It has the characteristic perianal tubercles and apical disc structure of that family, and also has a similar style of ambulacral plate compounding. The sphaeridial pits are shallow and clearly convergent with those in Hyposalenia.
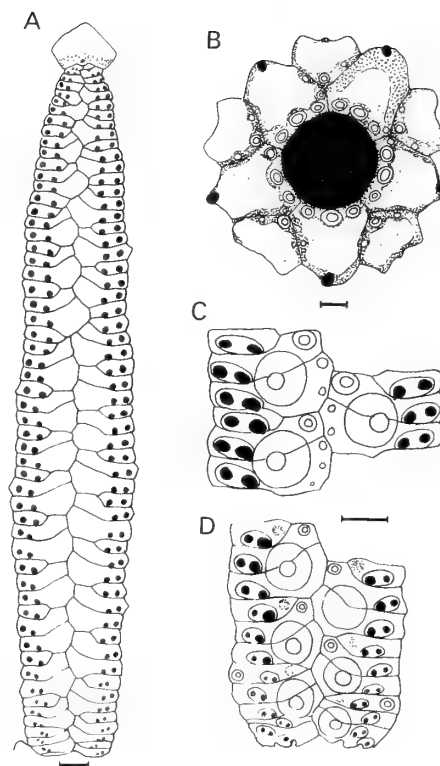
Fig. 22   Camera lucida drawings of plating in *Glyphopneustes hattaensis* Ali. **A,** Ambulacral plating, from ocular plate (top) to peristome margin (bottom), BMNH EE3926; **B,** apical disc, BMNH EE3912; **C,** ambital ambulacral plating, BMNH EE3915; **D,** adoral ambulacral plating, peristomial border at bottom, BMNH EE3915. Scale bars = 1 mm.

Family **ARBACIIDAE** Gray, 1835
Genus *CODIOPSIS* Agassiz, 1840

Codiopsis lehmannae sp. nov Pl. 9, figs 1–2; Pl. 12, figs 1–3; Fig. 23

DERIVATION OF NAME.   After Mrs C. Lehmann, the finder of the holotype.

TYPES.   Holotype, BMNH EE5033; paratypes (both incomplete test fragments), BMNH EE3439, EE3440.

OCCURRENCE.   One specimen comes from Bed 15, section 1, Jebel Buhays, a second comes from bed 10 (top), section 2, Jebel Rawdah. The third specimen was found loose in the basal scree at Jebel Rawdah, section 2, and is almost certainly derived from the lowest few metres of the Simsima Formation (beds 3–10).

DESCRIPTION.   The holotype is 18·3 mm in diameter and 8·2 mm in height (45% of the diameter). The two other specimens are larger, but incomplete, and by estimation would have been around 35–40 mm in test diameter. The base is flat, the upper surface domal, and the ambitus is very sharp and at the base. The apical disc is preserved in BMNH EE3440 and EE5033. It is dicyclic and firmly fixed to the corona (Pl. 12, fig. 1; Fig. 23C). The periproct is oval and 1·7 mm in diameter in the 18·3 mm diameter individual (9·3%).
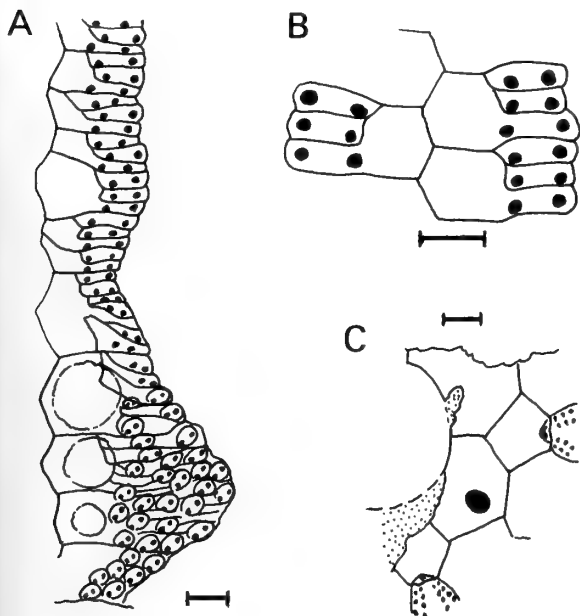
Fig. 23 Camera lucida drawings of plating in *Codiopsis lehmannae* sp. nov. **A,** ambulacral plating (one column only) from supra-ambital region (top) to peristomial margin (bottom), BMNH EE3439; **B,** aboral ambulacral plating, a little above the ambitus, BMNH EE3439; **C,** apical disc (incomplete) showing parts of two genital plates and two ocular plates, BMNH EE3440. Scale bars = 1 mm.

Ambulacra are narrow and parallel-sided above the ambitus, where they are trigeminate. Plate compounding is arbaciid in style with two demiplates (Fig. 23B). There is a single calcitic pustule on each triad (Pl. 9, figs 1, 2). Pores are small and widely-spaced, possibly conjugate (though preservation is too poor to be certain). Below the ambitus the pore-pairs reduce in width markedly (Fig. 23A) and the ambulacra widen into extensive phyllodes. The pore-pairs adorally are crowded and circular in outline with well-developed periporal muscle attachment areas. Compounding becomes polygeminate in a complex fashion (Fig. 23A) and there is a single large tubercle on each compound plate.

Interambulacral plates are geniculate at the ambitus and adoral portions bear a single primary tubercle. This arrangement creates a row of slightly downward-facing tubercles along the ambitus (Pl. 9, figs 1, 2). Adradial portions of these plates have fine secondary tuberculation. Adradial to the primary tubercles and continuing adapically along the adradial margin are very large calcite pustules. These reduce in size considerably above the ambitus and appear to continue adapically at least most of the way to the apical disc. The remainder of the adapical plates may have a pitted epistroma (traces are seen in BMNH EE3439), but the test is not well preserved.

REMARKS. There is no doubt as to the generic placement of these specimens, on account of their distinctive pustules and arbaciid-style ambulacral compounding. Their sharp ambitus, flat base, extensive phyllodes and ambital ring of interambulacral tubercles are distinctive and are features unknown in other species. It differs from *Codiopsis brunei* Lambert, from the Maastrichtian of Maastricht, in being very much larger

and in lacking well-developed aboral pustules. It comes closer to *C. disculus* Peron & Gauthier (and its synonyms *C. stephensoni* Cooke and *C. fontei* Vidal) from the late Campanian/Maastrichtian of Algeria, southern Spain, Senegal, Brazil and southern U.S.A., but differs from that species in having a more depressed profile, sharper ambitus and more distinct ambital ring of large tubercles. In *C. lehmannae* the primary interambulacral tubercles form a peripheral row, whereas in *C. disculus* the tubercles form a V-shaped arrangement extending adorally. Finally, in *C. lehmannae* the peristome appears highly scalloped.

Genus *HATTOPSIS* Ali, 1992

Hattopsis sphericus Ali, 1992 Pl. 9, figs 3–8; Pl. 10, figs 1, 2, 4; Fig. 24, 25B–D, 26B, 27A

1992b *Hattopsis sphericus* Ali: 694, fig. 3.

TYPES. Holotype 910401 in the Museum of the Geology Department, University of Al Ain, United Arab Emirates. Paratype 910402.

MATERIAL STUDIED. 73 specimens, of which the biometric data was taken from the following: BMNH EE3658, EE3663, EE3690, EE3692–95, EE3698, EE3702, EE3705, EE3707–20.

OCCURRENCE. The species was described from Jebel Rawdah (?section 1) by Ali (1992). Material collected *in situ* is as follows:
Jebel Faiyah, section 1: bed 7 (1); bed 8 (pycnodont level) (8).
Jebel Rawdah, section 1: bed 3 (22); bed 4, mostly towards top and base of bed 5 (44).
Jebel Rawda, section 2: bed 11 (2); loose in scree at base of section (1).

DIAGNOSIS. A spherical arbacioid with a reticulate epistromal ornamentation. Every third ambulacral pore-pair reduced in size. Two interambulacral tubercles on each plate. Peristomial rim elevated as a lip interradially.

DESCRIPTION. Tests range from 12·0 to 20·8 mm in diameter (Fig. 24) and are circular to rounded pentagonal in outline. Test height is 60–83% of the diameter (mean = 74%, SD = 6·5%, N = 16), and tests are globular in profile with a small base and apex (Pl. 10, fig. 2).

The apical disc is dicyclic and occupies 23–33% of the test diameter (mean = 27%, SD = 2·4%, N = 14). The periproct is oval in outline and 9–12% of the test diameter in diameter. Ocular plates project slightly beyond the ring of genital plates (Pl. 10, fig. 2; Figs 25B, C). Genital plates are large and flat except around the periproctal margin where they are raised to form a rim. All genital plates are similar in size. The madreporite pores extend over most of genital plate 2. Well-preserved specimens show a reticulate pattern of ridges and pits (Pl. 10, fig. 2).

Ambulacra are 20–24% of the test diameter in width at the ambitus (Fig. 24). They are compound throughout with trigeminate plating. Close to the peristome both upper and lower elements are demiplates, but elsewhere it is only the upper element that is a demiplate (Fig. 26B). This demiplate has a pore-pair that is very much smaller than those on the other two elements. Each triad has a single large primary
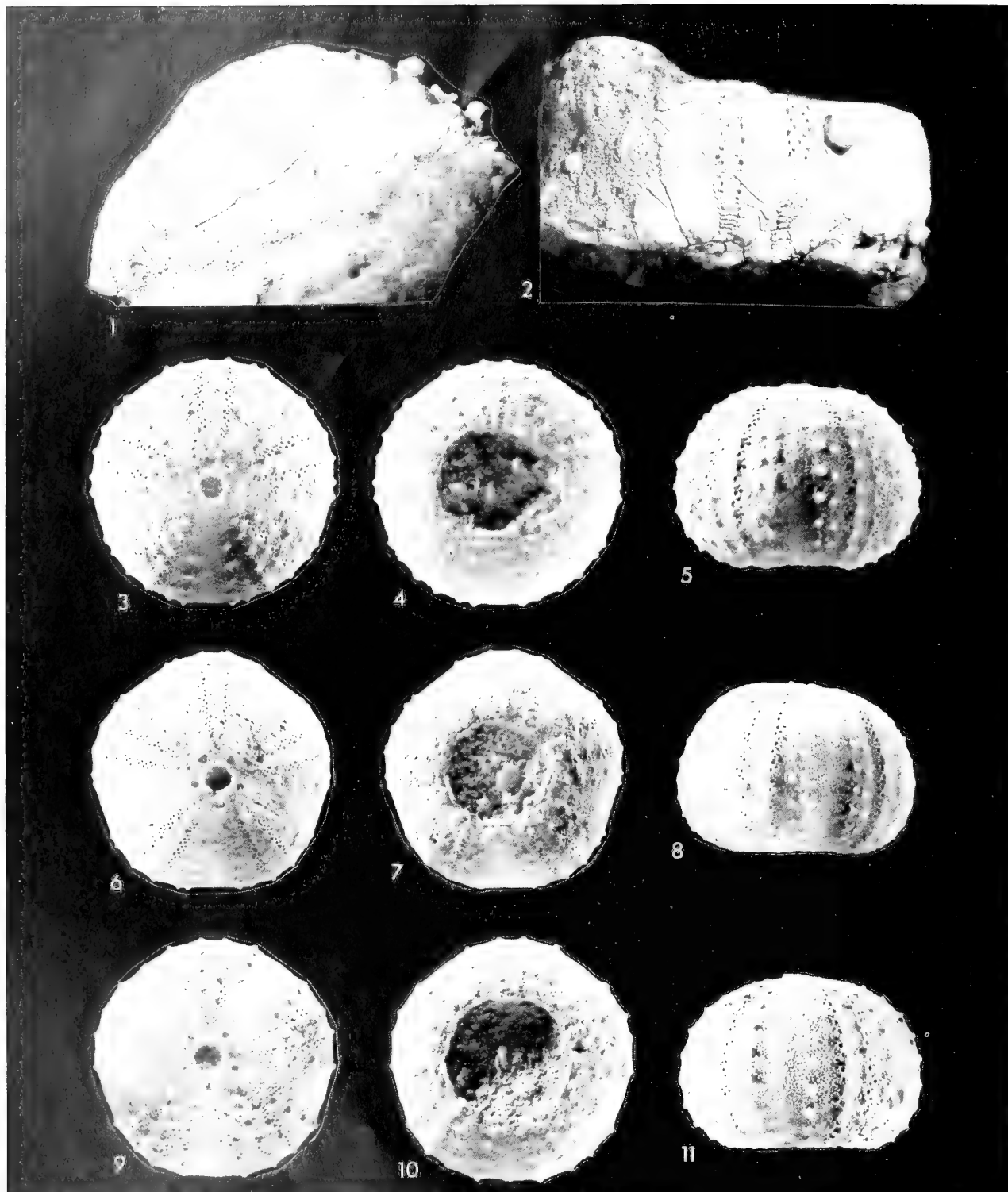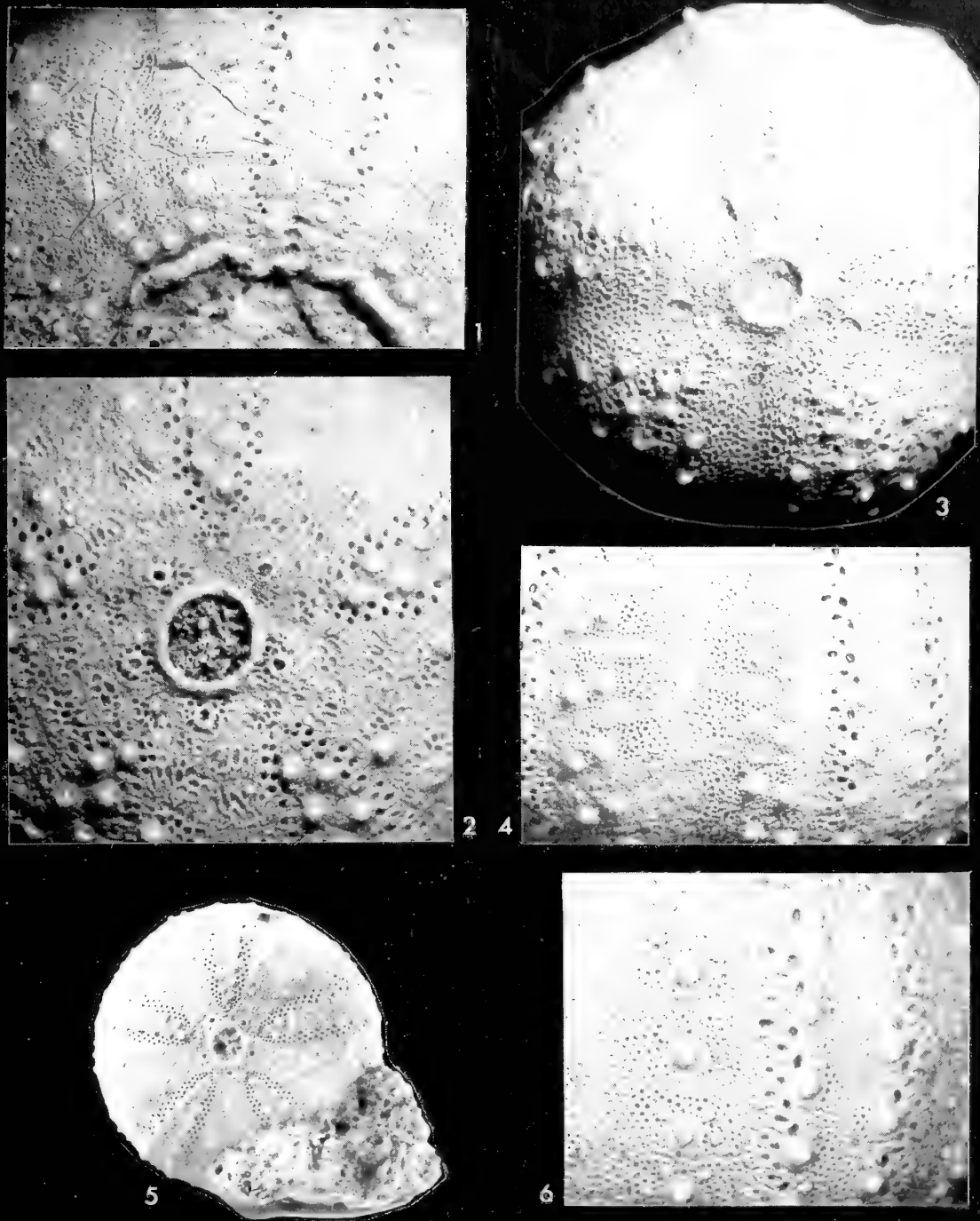
PLATE 10

Figs 1, 2, 4 *Hattopsis sphericus* Ali. BMNH EE3660; **1**, adoral detail showing sphaeridial pits at perradius and peristomial lip, × 6; **2**, apical disc, × 6; **4**, detail of ambital interambulacrum, × 6. Jebel Faiyah, section 1, bed 11.

Fig. 5 *Noetlingaster paucituberculatus* (Noetling). BMNH EE3680, juvenile, apical view, × 4 (see also Pl. 11, Figs 4, 5). Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation.

Figs 3, 6 *Hattopsis paucituberculatus* sp. nov. **3**, BMNH EE3672, paratype, adapical detail, × 7. Jebel Faiyah, section 1, bed 2. **6**, BMNH EE3682, paratype; ambital detail, interambulacrum to left, × 6. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation.

tubercle. There is a small secondary tubercle on the perradial margin of the lower element but other miliaries and secondary tubercles are absent. The perradius is ornamented with a reticulate pattern of ridges and shallow pits (Pl. 10, fig. 4). Close to the peristome there are up to four sphaeridial pits arranged uniserially down the perradius (Pl. 10, fig. 1). There are 33 pore-pairs and 10 primary tubercles in an ambulacral column at 12 mm test diameter, rising to 45–50 pore-pairs and 14–16 primary tubercles at 20–21 mm diameter (Fig. 24). No phyllodes nor any hint of pore-pair crushing is seen towards the peristome, and the pore-pairs themselves become much smaller adorally (Pl. 9, figs 4, 7; Fig. 26B).

Interambulacra are 36–40% of the test diameter in width at the ambitus. Plates are wider than tall and carry two small primary tubercles placed towards the adradial margin (Pl. 10, fig. 4; Fig. 27A). The tubercles in each pair are contiguous but are well separated from pairs of tubercles on other plates. There are no secondary or miliary tubercles, the remainder of the plate being covered in the same reticulate ornament of ridges and pits. At the peristome edge the interambulacra are thickened to form a distinct lip (Pl. 10, fig. 1). There is a single T-shaped primordial interambulacral plate forming the border to the peristome (Fig. 25D). There are 11 interambulacral plates in a column at 12 mm diameter, rising to 14 or 15 at 20–21 mm test diamater (Fig. 24).

The peristome is not at all invaginated and is 38–48% of the test diameter across (mean = 43%, SD = 3·1%, N = 13). Buccal notches are very slight and the raised interambulacral rim forms the most prominent feature (Pl. 10, fig. 1).

REMARKS. Ali (1992b) gave a detailed description of this species but new features reported here for the first time
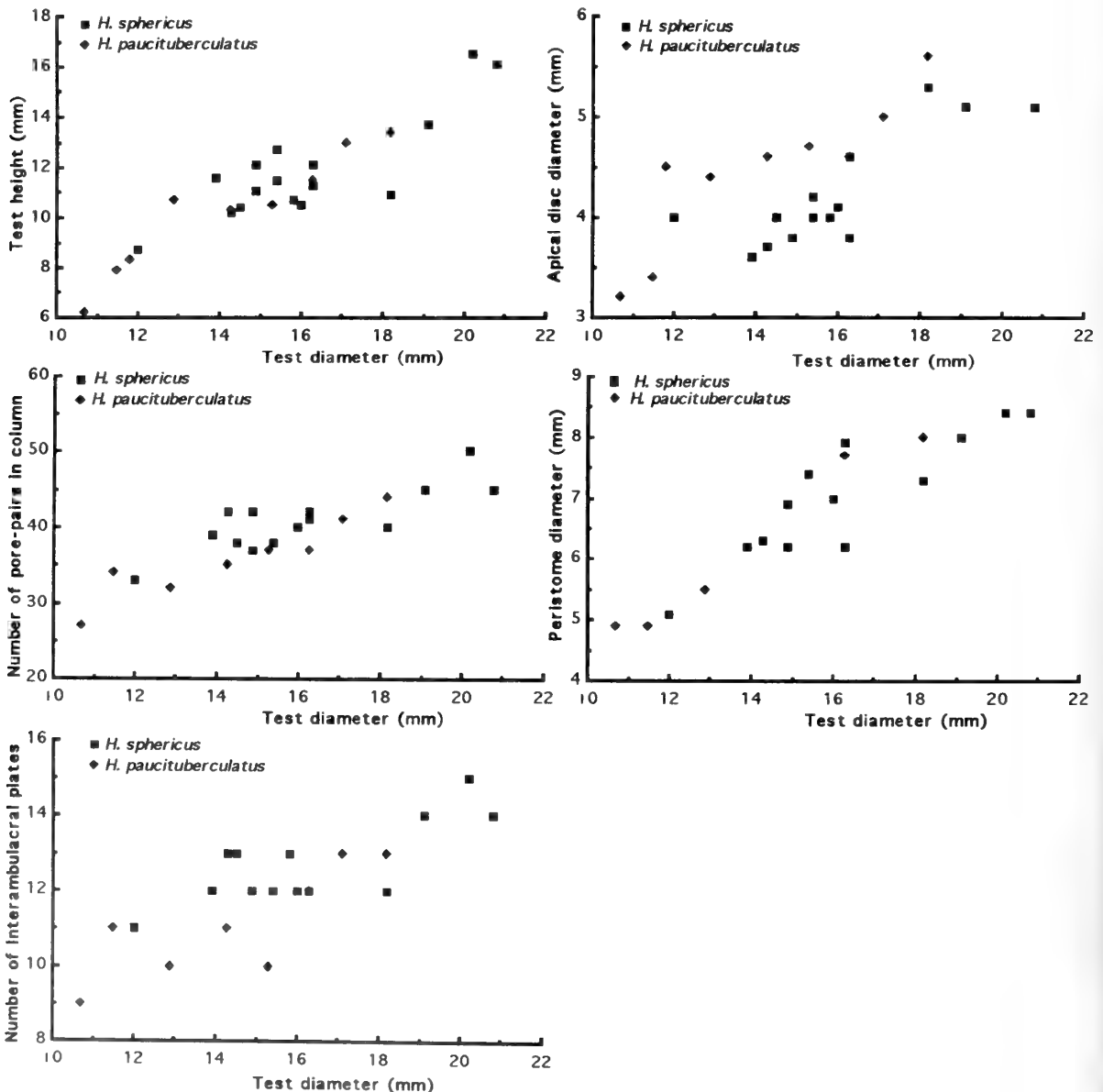
Fig. 24   Biometric data for *Hattopsis sphericus* Ali and *Hattopsis paucituberculatus* sp. nov.

include the perradial uniserial row of sphaeridial pits, the large T-shaped primordial interambulacral plate and the extensive development of reticulate ornamentation. The primordial plate, the uniserial and perradially positioned sphaeridial pits and the style of ambulacral compounding clearly place *Hattopsis* in the Arbaciidae. The reduction of one pore-pair in each triad and the presence of primary interambulacral tubercles above the ambitus separate *Hattopsis* from *Codiopsis*, which it resembles. *Hattopsis* comes most close in structure and appearance to juveniles of *Noetlingaster*, but differs from them in having fewer interambulacral tubercles at comparable sizes, and in being more globular in profile.

Hattopsis paucituberculatus sp. nov. Pl. 9, figs 9–11; Pl. 10, figs 3, 6; Pl. 11, fig. 9; Figs 24, 25A, 26A, 27B

TYPES. Holotype EE3683, paratypes, EE3682, EE3678, EE3688, EE3684–85.

MATERIAL STUDIED. There are 22 specimens in addition to the types. Biometric data is based on the following specimens: BMNH EE3672, EE3675, EE3678–79, EE3682–85, EE3688.

OCCURRENCE. This species was found at the following localities and horizons:
Jebel Faiyah, section 1: bed 2 (12).
Jebel Buhays section 1: in scree derived from lowest beds of the Simsima Formation (11); base of bed 12 (1).
Jebel Buhays, section 2: loose in scree, derived from lowest 3 m of the Simsima Formation (1).
Jebel Buhays, section 3: basal beds of the Simsima Formation (2).
Jebel Aqabah: bed 1 (1).
Jebel Rawdah, section 2, bed 8 (1); loose in scree derived from lowest part of section (1).

DIAGNOSIS. A species of *Hattopsis* with only a single interambulacral tubercle on each interambulacral plate at all sizes.

DESCRIPTION. Tests are 6·2 to 18·2 mm in diameter and circular to rounded pentagonal in outline (Pl. 9, figs 9–11). Test height is 58–83% of test diameter (mean = 71%, SD = 6·7%, N = 9) and in profile the test appears globular.
The apical disc is dicyclic, like that of *H. sphericus* (Fig. 25A). It is 28–37% (mean = 31%) of test diameter in diameter and there is an elevated rim around the periproct margin (Pl. 10, fig. 3). Gonopores are generally rather larger and more oval than those of *H. sphericus*.
Ambulacra are 20–25% of the test diameter in width at the ambitus and the ambulacral compounding is as in *H. sphericus* (Fig. 26A). There are 27 pore-pairs and 8 tubercles in a column at 10·7 mm test diameter, rising to 44 pore-pairs and 14 tubercles at 18·2 mm test diameter (Fig. 24). Aborally from the ambitus, the pore-pair on the upper demiplate in each triad is greatly reduced in size (Pl. 10, fig. 6; Fig. 26A). Adorally all pore-pairs become small and they remain uniserial to the peristome edge.
Interambulacra are 36–39% of the test diameter in width. Each plate carries a small primary tubercle, situated towards the adradial margin. (Pl. 10, fig. 6; Fig. 27B). The remainder of the plate is covered in fine reticulate ridges and pits. There are no secondary tubercles developed, even in the largest specimens.
The peristome is 43–47% of the test diameter in diameter
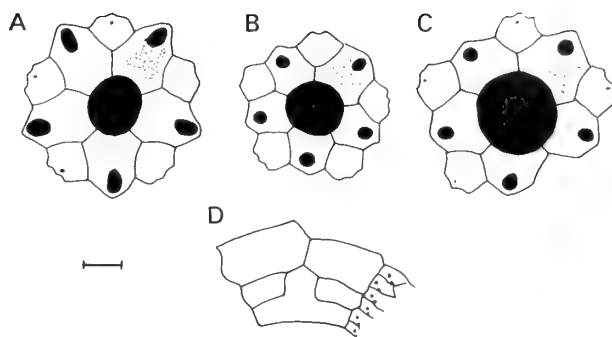
Fig. 25 Camera lucida drawings of plating in *Hattopsis*. **A-C**, apical discs; A, *H. paucituberculatus* sp. nov, BMNH EE3672; B, *H. sphericus* Ali, BMNH EE3692; C, *H. sphericus* Ali, BMNH EE3681. **D**, *H. sphericus*, BMNH EE3693, adoral interambulacral plating, peristomial edge at base. Scale bar = 1 mm.
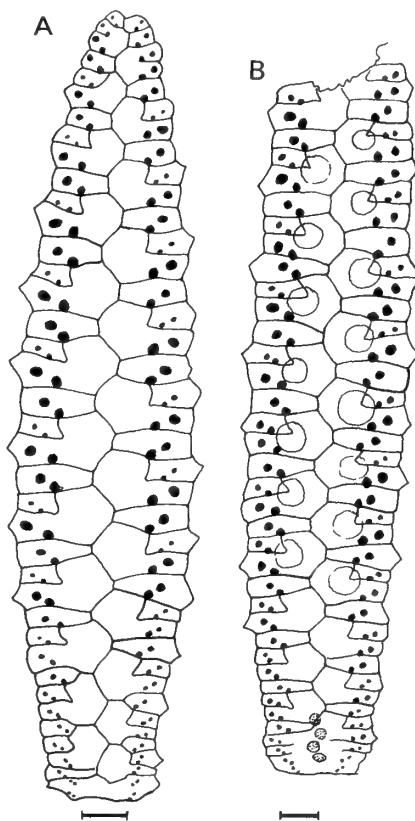
Fig. 26 Camera lucida drawings of ambulacral plating in *Hattopsis*. **A**, *H. paucituberculatus* sp. nov., complete ambulacrum from apical disc (top) to peristomial margin (bottom); BMNH EE3678; **B**, *H. sphericus* Ali, ambulacrum from close to apical disc (top) to peristomial margin (bottom); BMNH EE3659. Scale bars = 1 mm.

and has the usual interambulacral lip and shallow buccal notches.

REMARKS. This species resembles *H. sphericus* in all details except that it has only a single interambulacral tubercle on each plate, rather than the two found on all specimens of *H. sphericus* greater than 12 mm. Although I have included
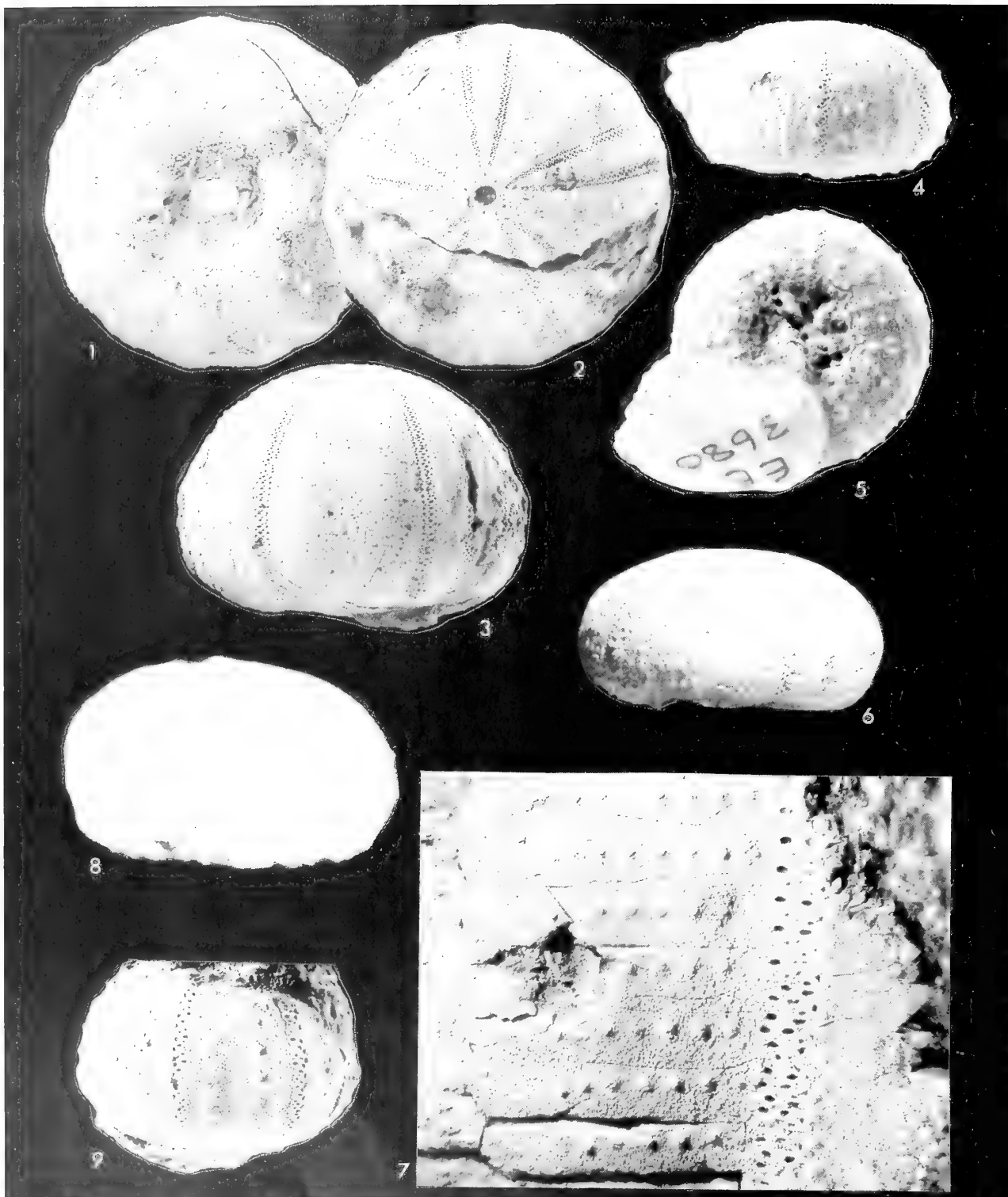
Figs 1–3 *Noetlingaster emiratescus* Ali. BMNH EE3285; **1**, oral; **2**, apical; **3**, lateral; all × 1. Jebel Rawdah, section 4, bed 12.

Figs 4–7 *Noetlingaster paucituberculatus* (Noetling). **4, 5**, BMNH EE3680 (juvenile); **4**, lateral; **5**, oral; both × 4. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation. **6**, BMNH EE3286 (juvenile), lateral view, × 4. Jebel Rawdah, section 2, bed 11. **7**, BMNH EE3282, detail of ambital region, adoral towards top and interambulacrum to left, × 4.

Fig. 8 ?*Noetlingaster* sp BMNH EE3689, lateral, × 5. Jebel Huwayyah, section 2, beds 2–7.

Fig. 9 *Hattopsis paucituberculatus* sp. nov. BMNH EE3682, lateral view, × 3. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation.

some specimens smaller than 12 mm in this species, they could possibly turn out to be juveniles of *H. sphericus*. However, the majority of specimens are larger than 12 mm and the distribution of the two species is also not the same. Whereas *H. sphericus* is found predominantly at Jebel Rawdah, section 1, beds 3–4 and also in beds higher up the succession (bed 11) in section 2, as well as at the pycnodont level (bed 8) at Jebel Faiyah, *H. paucituberculatus* consistently occurs further down in the succession (basal beds of Jebel Buhays and Jebel Faiyah, and bed 8 in Jebel Rawdah, section 2). The two species are thus stratigraphically discrete.

Genus *NOETLINGASTER* Vredenburg, 1911

TYPE SPECIES. *Protechinus paucituberculatus* Noetling, 1897 by original designation.

REMARKS. *Noetlingaster* has previously been classified in the Stomechinidae on account of its imperforate tuberculation and dicyclic apical disc (e.g. Fell & Pawson 1966). However, it has a single large primordial interambulacral plate at the adoral end of each interambulacrum and a tuberculation style very similar to that of *Hattopsis*. Primordial interambulacral plates this well-developed are known only in the Arbaciidae. Finally, juvenile forms of *Noetlingaster* are extremely similar in appearance to *Hattopsis*, differing only in having a more depressed test profile and more interambulacral tubercles at corresponding sizes. Given the marked similarity between *Hattopsis* and *Noetlingaster* in apical disc, tuberculation, interradial epistroma and pore-pair development, there seem strong grounds for placing *Noetlingaster* as an arbaciid.

There are nine named species of *Noetlingaster*, all from the late Cretaceous. The type species *N. paucituberculatus* (Noet-

Fig. 27 Camera lucida drawings of ambital plating in *Hattopsis* and *Noetlingaster?* sp.: interambulacral plate on the left, ambulacral plate on the right. **A,** *Hattopsis sphericus* Ali, BMNH EE3693; **B,** *Hattopsis paucituberculatus* sp. nov., BMNH EE3683; **C,** *Noetlingaster?* sp., BMNH EE3689.

ling, 1897) comes from horizon 4 (?Maastrichtian) in the Des Valley, Mari Hills, West Pakistan. Other species are: *N. emiratescus* Ali (1989), described from Jebel Rawdah, western Oman mountains; *N. sanfilippoi* Checchia-Rispoli (1930), *N. millosevichi* Checchia-Rispoli (1930) and *N. lamberti* Checchia-Rispoli (1930), all from the Maastrichtian of Gebel Misid, Tripolitania, Lybia; *N. globulus* Devries (1967) and *N. hemisphericus* Devries (1967), both from the Maastrichtian of Kahta, Turkey; *N. monteili* Gauthier (1901) from the 'Senonian' south of Bilma, Algeria; and *N. boulei* Lambert (1906) from the Maastrichtian of Marohite, Madagascar. Devries (1967) reviewed previous species and discussed their diagnosis. He laid particular emphasis on the arrangement of interambulacral tubercles, recognizing two groups: those with a single row of interambulacral tubercles on each plate, and those with a double row. He pointed out that the actual number of tubercles in each row varied ontogenetically and also according to position on the test.

All these species are closely related because of their highly distinctive ambulacral plate compounding and pore-pair arrangement (see below). However, all have been erected on the basis of very few specimens, often simply the holotype. Thus the intraspecific variability has never been properly documented. In addition, the relatively thin test means that specimens are rarely well preserved. The large collection of specimens from Jebel Rawdah allows ontogenetic variability to be assessed in this species complex for the first time.

There are significant differences in size between the species that have been erected, and these may account for some of the morphological variation described. *N. boulei* is described from the smallest specimen, only 49 mm in diameter. *N. globulus*, *N. hemisphericus* and *N. emiratescus* are all based on specimens ranging from 65–83 mm. The remainder are described from large individuals between 95 and 120 mm in diameter (Fig. 28). As many of the characters previously used for species discrimination can be shown to vary with size in the Omani populations, it is important that similar-sized individuals are compared when differentiating species.

Shape differences were used by Devries (1967) to separate some species. He identified species as either 'subconical' or 'rounded convex'. However, there seems to be considerable variation in this feature within the sample described here, and thus the character has little worth. It is also difficult to use in practice since specimens are often crushed or distorted during preservation.

Ambulacral differences have also been used for diagnosing species. *N. boulei* for example has just one primary tubercle on ambulacral plates, and this is found on alternate plates only. However, as Lambert's (1906) photographs show, ambulacral tuberculation is not consistent. Adoral compound plates all have a single primary tubercle, whereas, adapically, tuberculation is more irregular with occasional plates lacking primary tubercles. Considering the small size of *N. boulei* one would not expect more than a single tubercle to be developed, by comparison with the Omani sample. Furthermore, tuberculation is very irregular in the Omani population, especially adapically from the ambitus where it is relatively common to find primary tubercles missing from ocassional plates. Such irregular ambulacral tuberculation characterises all species and from about 60 mm test diameter upwards all species have plates bearing two or three tubercles irregularly arranged. Note that although Gauthier (1901) describes *N. monteili* as having eight rows of ambulacral tubercles, his figures show only four irregular columns and the ambulacral
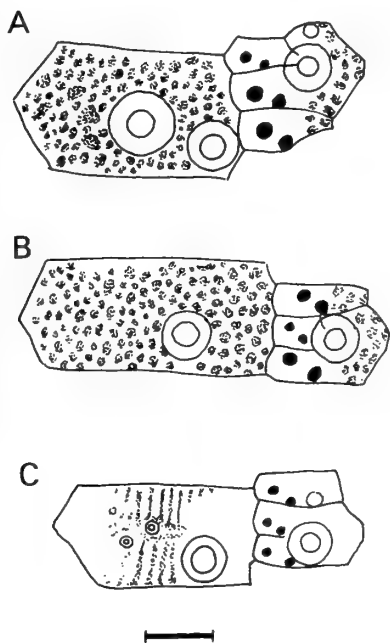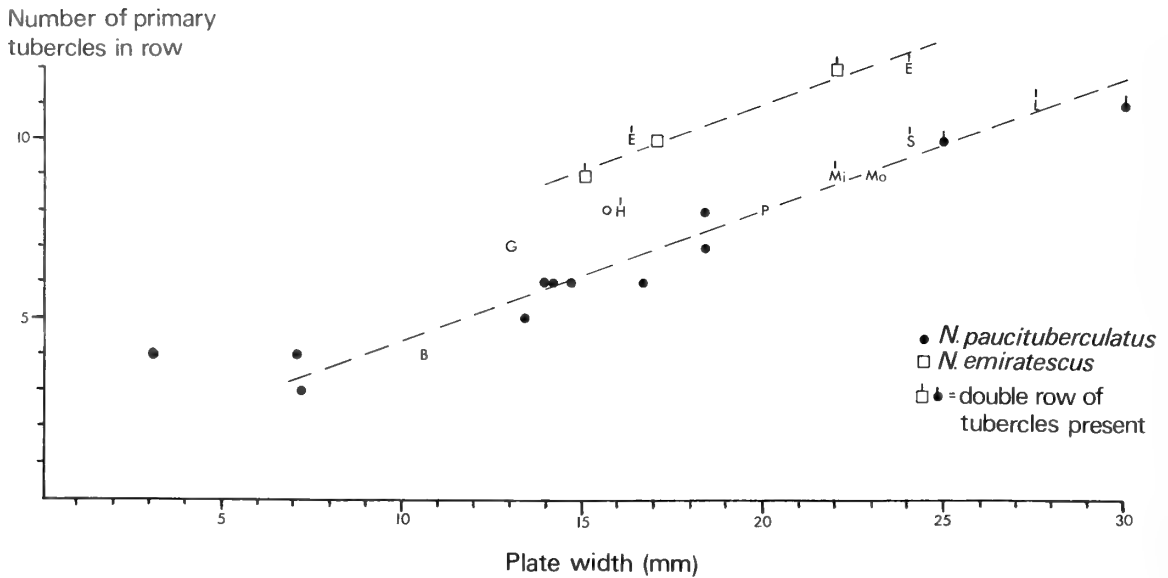
Fig. 28 Biometric data from *Noetlingaster* species. Type specimens for species are plotted as follows: B = *N. boulei* Lambert; E = *N. emiratescus* Ali (two syntypes); G = *N. globulus* Devries; H = *N. hemisphaericus* Devries; L = *N. lamberti* Checchia-Rispoli; Mi = *N. millosevichi* Checchia-Rispoli; Mo = *N. monteili* Gauthier.

structure does not differ from that seen in equivalent-sized Omani specimens.

Most emphasis has been placed on interambulacral tuberculation for differentiating between species. Devries (1967) recognized two species groups: those with just a single row of tubercles to each interambulacral plate and those with a double row. He also distinguished between those with a naked interradial zone of fine granulation and those with primary tubercles extending more or less to the interradius. Unfortunately, the Omani specimens also show considerable variation in these features. The majority simply have a single row of primary tubercles extending more or less to the perradius. From the ambitus adapically there may or may not be a naked zone free of primary tubercles and when present this zone may or may not extend below the ambitus. In many specimens it is difficult to observe tuberculation interradially because of weathering, and the same is probably true for the specimens on which other species are based. Single rows of tubercles are characteristic of *N. paucituberculatus*, *N. monteili*, *N. boulei* and *N. globulus*, whereas *N. sanfilippoi*, *N. millosevichi*, *N. hemisphaericus* and *N. emiratescus* all have two or three additional tubercles forming a second row adradially, and *N. lamberti* has a full double row of tubercles developed on all plates. All tuberculation styles, except that seen in *N. lamberti*, are encountered in the Omani sample. As can be seen from Fig. 28, there is a strong correlation between the number of tubercles on a plate and the plate width (which is proportional to test diameter). Furthermore, it is primarily the larger specimens that have a second row of tubercles developed adradially. However, it is not completely size-dependent since the 69 mm diameter specimen EE3279 has a well developed secondary row of tubercles whereas others of that size do not.

In conclusion, the variation observed within the 20 reasonably well-preserved specimens from the western Oman mountains is almost as great as that observed between the nine described species, each based on one or a few specimens only. The presence or absence of an interradial naked zone and the extent of this zone when present, the number of interambulacral tubercles in a row in proportion to the plate width and the development of a second row of primary tubercles to a plate are all variable. Similar variation of tuberculation has been found in both Turkey (Devries 1967) and Libya (Checchia-Rispoli 1930), but was used to distinguish 'species'.

By contrast the analysis of variation amongst Omani specimens suggests that tuberculation pattern may not be so rigidly developed. It does, however, support some subdivision of the genus. When tuberculation style is plotted against test diameter, two distinct growth trajectories emerge for Omani specimens (Fig. 28). In some specimens there are numerous densely-spaced tubercles with secondary tubercle rows present, even at 60 mm test diameter. Other specimens have more widely-spaced primary tubercles and only develop a secondary row of adradial tubercles on ambital plates at a very large size. Although these may simply represent end members of a continuous spectrum, the small sample does not indicate any significant overlap. Those with many tubercles also always lack a granular interradial zone, whereas those with relatively fewer tubercles typically have a naked zone. However, the development of this naked zone is quite variable, with some specimens showing a broad zone extending almost to the peristome, and others with the zone restricted to a narrow wedge-shaped area adapically. Measurements taken from the types of all nine species are plotted for comparison. The type species *N. paucituberculatus* falls into the growth series of forms with fewer tubercles, as do the types of *N. millosevichi*, *N. boulei*, *N. monteili*, *N. sanfilippoi*, and *N. lamberti*. The more densely tuberculate form corresponds to *N. emiratescus* and may also include *N. globulus* and *N. hemisphaericus,* although both plot in an intermediate position. (This may be due to inaccuracies in the magnifications for the camera lucida drawings of interambulacral plates given approximately by Devries (1967, pl. 2)).

Plotting those with a secondary row of tubercles to interambulacral plates shows that the secondary row appears at about 15 mm plate width in *N. globulus/N. emiratescus*, whereas it only develops at around 22 mm plate width in the *N. paucituberculatus* group.

The one anomolous specimen is BMNH EE3282, which has numerous small interambulacral tubercles, but a wide interradial granular zone. It falls in between the two growth series in Fig. 28.

In conclusion, only two species of *Noetlingaster* are recognized here:

(1) Forms to *ca.* 125 mm diameter with granular interradial zone developed adapically or throughout and a single row of relatively widely spaced interambulacral tubercles. Adradially, a second shorter row of tubercles is developed in larger specimens. These forms occur at Jebel Rawdah, section 2 from bed 11 to 14 and correspond to the form first described as *N. paucituberculatus* (Noetling).

(2) Forms to *ca.* 125 mm with a second row of interambulacral tubercles present adradially from about 60 mm test diameter, and no naked zone. At comparable sizes there are more interambulacral tubercles in a row than in the first species. This form occurs at Jebel Rawdah section 1, but at higher levels in the section than *N. paucituberculatus*. It has been described from the Oman Mountains under the name *N. emiratescus* Ali.

Noetlingaster paucituberculatus (Noetling, 1897) Pl. 10, fig. 5; Pl. 11, figs 4–7; Figs 28, 29, 30A–D, F, H, 31

1897 *Protechinus paucituberculatus* Noetling, 1897: 16, pl. 2, fig. 3, pl. 3, fig.1.
1898 *Noetlingia paucituberculata* Noetling; Lambert: 126.
1901 *Noetlingia Monteili* Gauthier: 191, pl. 3, figs 1–3.
1906 *Noetlingia Boulei* Lambert: 11, pl. 2, fig. 7.
1911 *Noetlingaster paucituberculata* Noetling; Vredenburg: 46.
1930 *Noetlingaster Millosevichi* Checchia-Rispoli: 14, pl. 2, figs 1, 2, pl. 4, figs 3, 4.
1930 *Noetlingaster Sanfilippoi* Checchia-Rispoli: 6, pl. 1, fig. 1, pl. 3, fig. 2, pl. 4, fig. 2.
1930 *Noetlingaster Lamberti* Checchia-Rispoli: 20, pl. 1, fig. 2, pl. 3, fig. 1, pl. 4, fig. 1.

TYPES. The type is the 95 mm diameter specimen described by Noetling (1897) from the late Cretaceous of the Mari Hills, West Pakistan.

MATERIAL STUDIED. 19 relatively complete tests and 2 test fragments, including juveniles. The following ten specimens were used in the biometric analysis: BMNH EE3267, 3269, 3271–75, 3280, 3282 and 3286.

OCCURRENCE. In the western Oman mountain area *N. paucituberculatus* was found at the following levels:
Jebel Rawdah section 1, base of bed 4 (juvenile).
Jebel Rawdah, section 2: bed 11 (3, plus fragments); bed 14 (5, plus fragments); bed 19 (2); bed 25 (4); bed 26 (2).
Jebel Buhays, section 1: loose in scree derived from lowest beds of the Simsima Formation (3, including one complete 13 mm diameter juvenile).

Outside the eastern Arabian peninsula this species is recorded from western Pakistan, Algeria, Libya and Madagascar.

DESCRIPTION. Tests range in diameter from 15 to 126 mm. They are more or less circular in outline, but very slightly depressed both interradially and adradially. Test height is 54–79% of test diameter (mean = 66%, SD = 7·2%, N = 10) and juveniles tend to have more depressed tests than adults. In profile the test is subconical, with a broad base, narrow apex and low ambitus (Pl. 11, figs 4, 6). The ambitus lies at about one quarter of the test height above the base.

The apical disc is relatively small, occupying only 13–16% of the test diameter in medium to large individuals (mean = 14%, SD = 1·2%, N = 6). It is proportionally larger in small individuals, occupying 19% of the test diameter in the 15 mm diameter specimen (Fig. 29). Disc plating is dicyclic (Figs 30A, B). The madreporite is very much larger than other genital plates and is densely covered in small pores. Each genital plate has a large oval gonopore which may be surrounded by a slight rim. The ocular plates are small and pentagonal, each with a small ocular pore. The periproctal opening is large and oval.

Ambulacra are straight and taper adapically. At the ambitus their width is 16–20% of the test diameter. Ambulacral plates are trigeminate throughout with a highly distinctive style of compounding (Figs 30C, D, F, H). The lowest element is large and occupies the full width. There is a smaller demi-plate above, which always carries a large pore-pair adradially and an even smaller, fully occluded element above that (Figs 30D, F). This arrangement is found along the entire length of the ambulacrum in all medium to large individuals, except at the very apex, where the occluded plate may reach the adradial suture. In smaller individuals both of the smaller elements are demiplates (Fig. 30H), while in BMNH EE3286, a juvenile of only 15 mm test diameter (Fig. 30F), the upper element extends to the perradial suture. There are no phyllodes nor any pore crushing towards the peristome. Each element carries a pore-pair, but only on the large primary element are these well-developed throughout (Pl. 11, fig. 7). The pore-pairs on the small occluded upper element are always reduced to rudimentary structures and in places may simply be represented by a single pore. The middle element usually has well-developed pore-pairs, but in larger individuals around the ambitus these may also be very much reduced in size (Fig. 30F). Pore-pair differentiation is hardly developed in the 15 mm diameter juvenile. Each compound plate usually carries a single primary tubercle close to the pore-zone. However, tuberculation is irregular and occasionally two tubercles occur to a plate. In the largest individuals most ambulacral plates carry two adradial primary tubercles, slightly offset on alternate plates. The perradial band is devoid of large tubercles above the ambitus, but this zone is relatively narrow, typically only some 15% of the interambulacral width. There are approximately 112 pore-pairs in a column at a test diameter of 32 mm, rising to around 180 at 80 mm test diameter (Fig. 29).

Interambulacral width at the ambitus is 41–47% of the test diameter. Plates are wide and low, and are slightly taller than ambulacral plates. There are 36 interambulacral plates in a column at 82 mm test diameter. The primary tubercle at the centre of the plate is set on a slight keel which runs down the midline of each column and is particularly prominent adapically. There are multiple small tubercles on each plate, three in the smallest individual (Pl. 11, fig. 4), rising to 11 in the
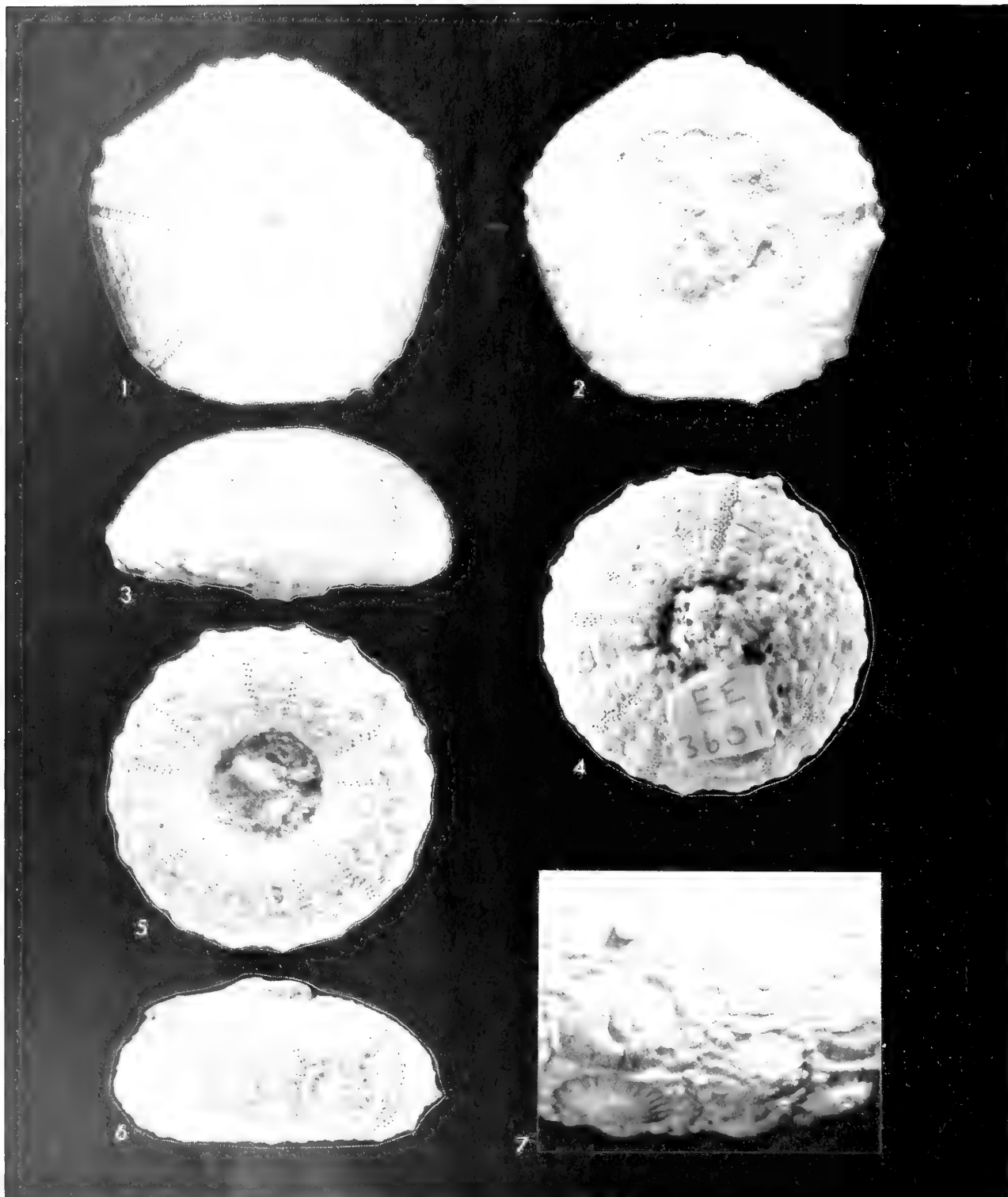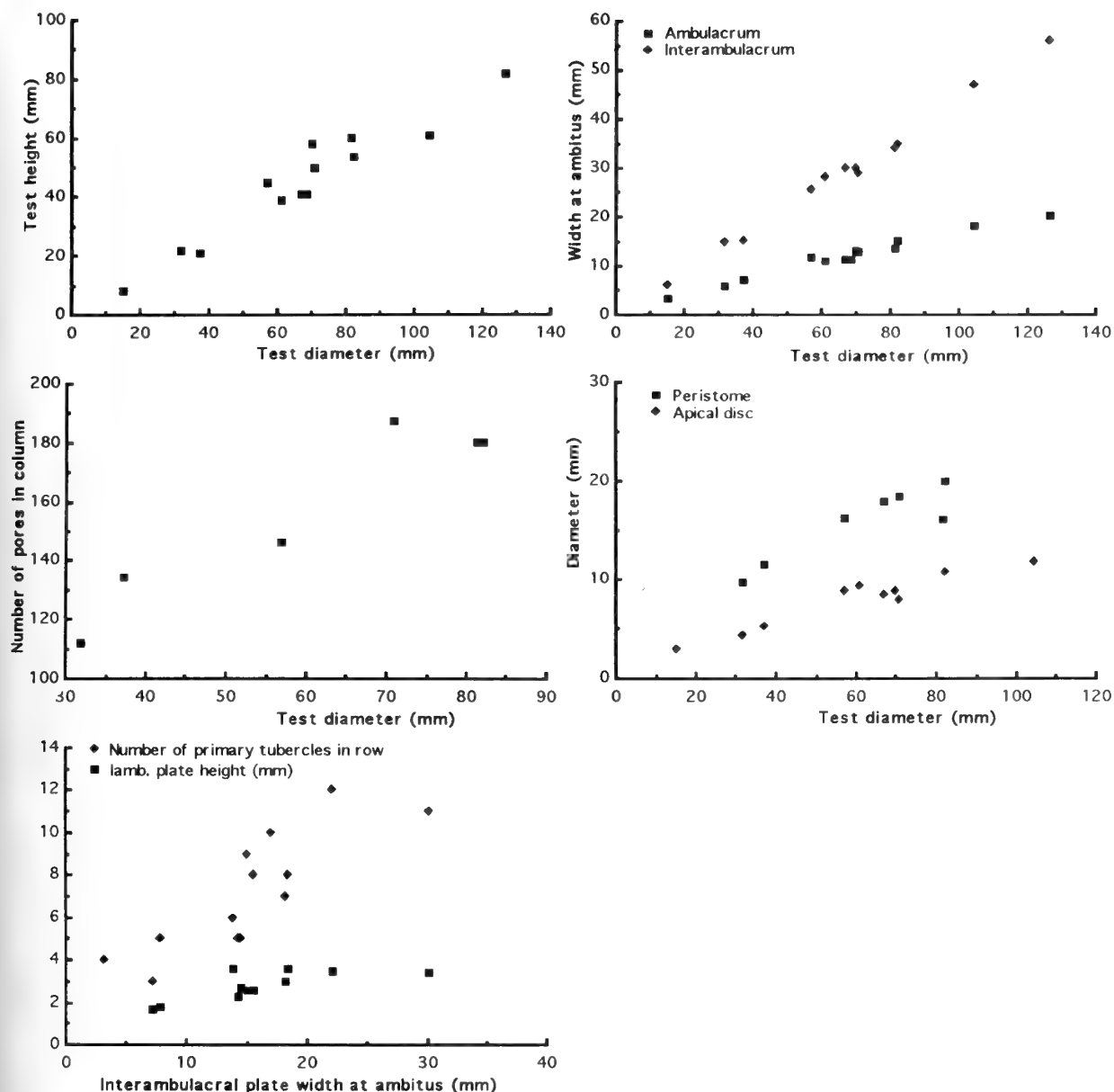
Fig. 29 Biometric data for *Noetlingaster paucituberculatus* (Noetling) and *N. emiratescus* Ali.

largest. These are arranged in a single, slightly arcuate row (Pl. 11, fig. 7), but the larger individuals may have two or three additional tubercles forming an upper row near the adradial suture. All tubercles are imperforate and non-crenulate and have relatively small mamelons and extensive areoles. Sutures between all plates are finely denticulate.

The peristome is very slightly sunken and is strongly indented by wide buccal notches. Peristome diameter is 20–31% of test diameter (mean = 27%, SD = 4·0%, N = 7).

REMARKS. This species is distinguished from *N. emiratescus* by its interradial granular zone, which may be small and developed only adapically, or may be broad and extend adorally. Within a single population from bed 14, section 2, Jebel Rawdah, the development of this granular zone was highly variable, with some having only a narrow adapical wedge of granules, others having a broad band extending adorally. It also differs from *N. emiratescus* in having fewer interambulacral tubercles at comparable sizes (Fig. 28). Smaller individuals (diameters less than *ca.* 100 mm) have single rows of tubercles on interambulacral plates, but a second row is present in larger specimens.

The species was first described by Noetling (1897) on the basis of a single specimen from West Pakistan. Gauthier (1901) later described a smaller, incomplete specimen of this species under the name *N. monteili* from the eastern Sahara region of Algeria. Other species that are probably best treated as synonymous are the three species described by Checchia–Rispoli (1930) from the Maastrichtian of Libya.
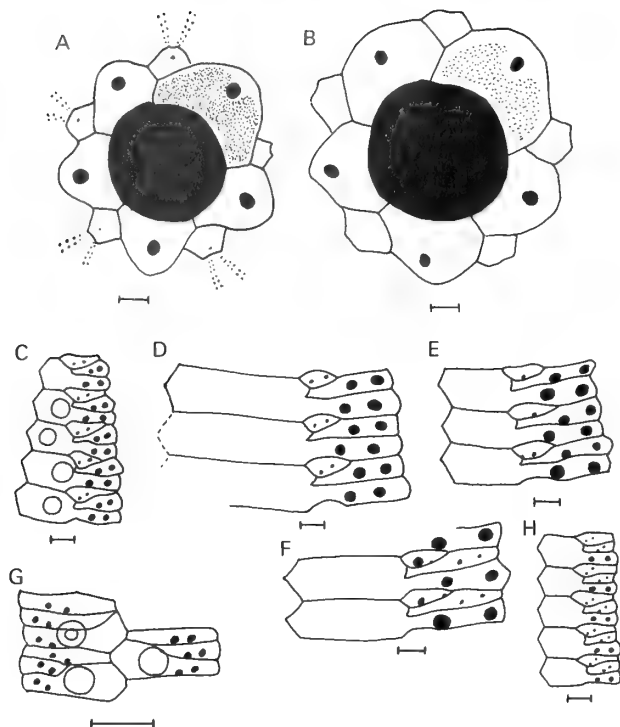
Fig. 30 Camera lucida drawings of *Noetlingaster*. **A-D, F, H,** *N. paucituberculatus* (Noetling): A, B, apical disc plating: A, BMNH EE3269; B, BMNH EE3275; C, adapical plating in a juvenile, BMNH EE5049; D, Ambital plating, BMNH EE3266; F, ambital plating, BMNH EE3286; H, adapical plating, BMNH EE3283. **E, G,** *N. emiratescus* Ali, BMNH EE3285; E, adapical plating; G, ambital plating. Scale bars = 1 mm.
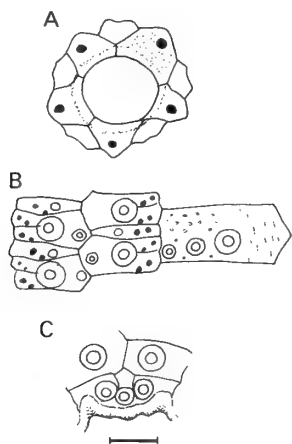
Fig. 31 Camera lucida drawings of plating in a juvenile *Noetlingaster paucituberculatus* (Noetling), BMNH EE3680. **A,** Apical disc; **B,** ambital plating, ambulacrum to the left, interambulcaral plate on right; **C,** adoral interambulacral plating, showing the single primordial interambulacral plate. Scale bar = 1 mm.

There is a general increase in size up the section at Jebel Rawdah, with small to medium-sized individuals found in the

lower beds and only large individuals towards the top in the deeper water facies.

Noetlingaster emiratescus Ali, 1989 Pl. 11, figs 1–3; Figs 28, 29, 30E, G

1989   *Noetlingaster emiratescus* Ali: 398, Fig. 2 (3–5)

TYPES. The types of *N. emiratescus* are three specimens and six fragments in the collections of the Geology Department, United Arab Emirates University, Al Ain.

MATERIAL STUDIED. Three specimens, BMNH EE3279, EE3284–85.

OCCURRENCE. All specimens, including the type material, come from Jebel Rawdah. The specimens reported here were collected from bed 4, Jebel Rawdah section 1 (1) and bed 13, Jebel Rawdah section 4 (2).

DIAGNOSIS. A *Noetlingaster* with smaller and denser interambulacral tubercles than other species, and completely lacking a naked interradial zone.

DESCRIPTION. Tests range from 68·5 to about 105 mm in diameter. In outline the interradii and adradii are slightly depressed. Test height is 58–71% of test diameter and in profile the test is inflated and subglobular. The ambitus lies about one third of test height above the base.

The apical disc occupies 11% of the test diameter and has the same arrangement of plates as *N. paucituberculatus*. Ambulacral structure is also more or less identical, with the pore-pair on the occluded plate rudimentary almost to the apex (Figs 30E, G). The middle pore-pair is also rudimentary from the ambitus adorally. Ambulacral tubercles are irregularly arranged and occupy the full width of the ambulacra, one or two to a compound plate.

Interambulacral plates are slightly V-shaped, with a single well-developed row of tubercles along the lower edge and a second, irregular row of occasional tubercles above. There are 19 tubercles in a row at a test diameter of 71 mm, rising to 13 at 105 mm test diameter (Fig. 28). Tubercles occupy the full width of plates throughout and there is no granular interradial zone as is found in *N. paucituberculatus*.

The peristome is small and somewhat invaginated, occupying 26% of the test diameter.

REMARKS. Ali (1989) described this species on the basis of the material collected from Jebel Rawdah. Its small, numerous interambulacral tubercles and lack of any interradial zone of granulation serve to separate it from the co-occurring species, *N. paucituberculatus*.

Noetlingaster? sp. (juvenile?)   Pl. 11, fig. 8; Fig. 27C

MATERIAL. One specimen, BMNH EE3689.

OCCURRENCE. From the *Loftusia* beds (beds 2–5), Jebel Huwayyah, section 2.

DIAGNOSIS. A species of arbaciid with a single primary interambulacral tubercle on ambital and adoral interambulacral plates, but smooth adapically. Ambulacral tubercles developed to apex. Broad ambital and adapical interradial zone ornamented with vertical riblets.

DESCRIPTION. The test is rounded pentagonal in outline and 13·2 mm in diameter. It has a broad flat base and domed

upper surface. Test height is 57% of test diameter and the ambitus lies at around 40% of test height.

The apical disc is 3·8 mm in diameter (29% of test diameter) and is dicyclic. It is not well preserved, but the genital plates are raised as a lip around the periproct margin and the periproct itself is 11% of the test diameter and oval in outline. Ocular plates protrude beyond the genital plates slightly.

Ambulacra are 20% of the test diameter in width at the ambitus. All plates are compound and trigeminate, but details of plate compounding are not clear. There is clearly a single element and a double element in each triad, but it is impossible to tell whether one of the double elements is a demiplate, as I suspect. All pore-pairs are equally well-developed. There is no phyllode development. There are 33 pore-pairs and 10 primary tubercles in a column.

Interambulacra are 39% of the test diameter in width at the ambitus. Each plate has a large adradial tubercle that extends adapically to within three or so plates of the apex. Adorally these tubercles lie subcentrally, but towards the apex they become positioned more and more closely towards the adradial suture. On ambital and adapical plates there is also a very much smaller mamelonate secondary tubercle lying at the centre of each plate within the zone of riblet ornamentation. The entire interradial zone from the ambitus upwards, has a well-developed ornamentation of vertically orientated riblets.

The peristome is 5·2 mm in diameter (40% of the test diameter) and is not invaginated. There are no raised interradial lips to the peristome margin. Buccal notches are extremely feeble.
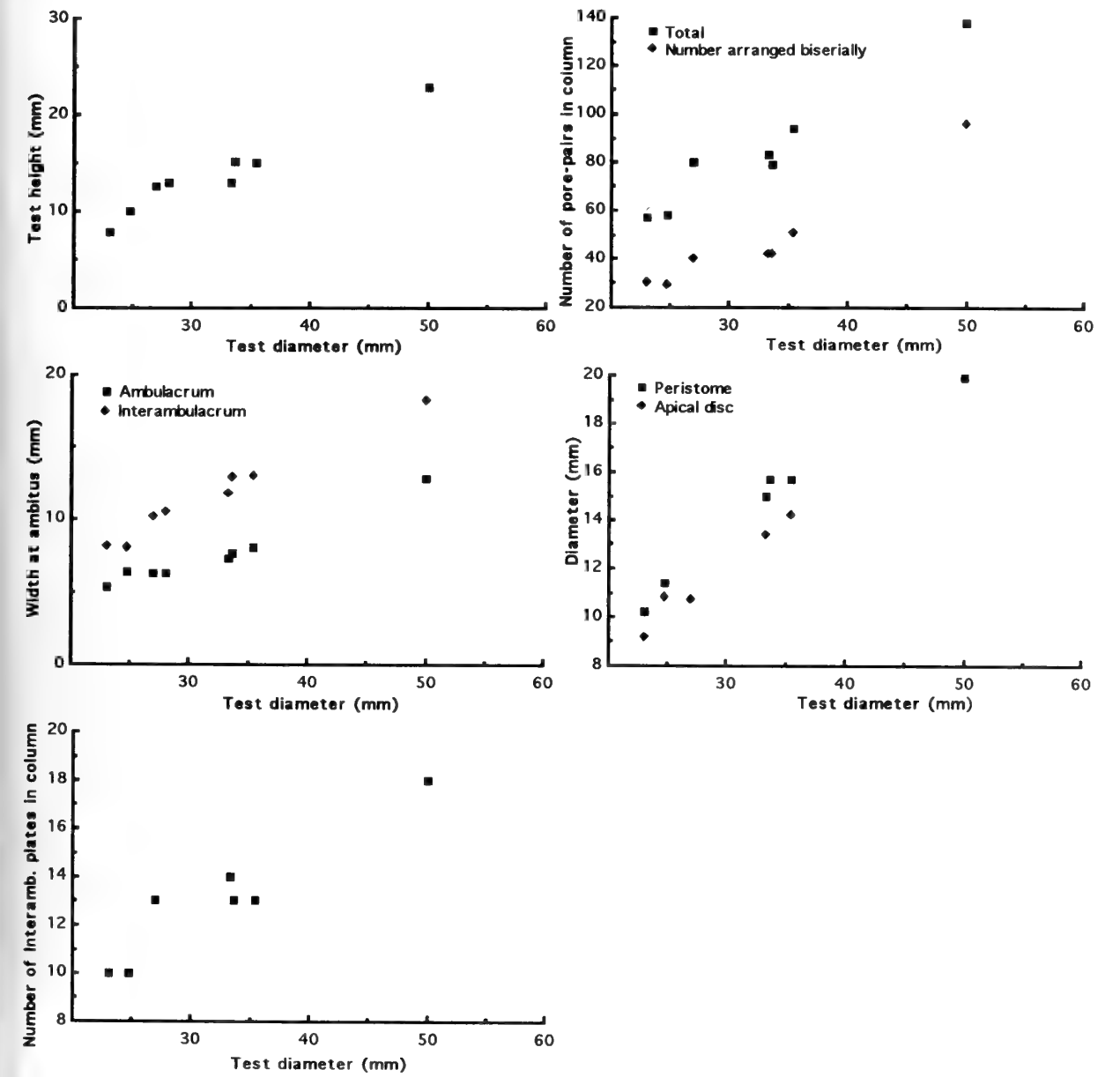
Fig. 32 Biometric data for *Phymosoma hexoaporum* Lambert.

REMARKS. This species is easily distinguished from *Hattopsis sphericus* on the basis of its interambulacral ornamentation of vertical riblets, and by its single row of primary interambulacral tubercles. It also lacks the reduced diameter pore-pair in each triad that is so characteristic of *H. sphericus* and *H. paucituberculatus*. It differs from *H. paucituberculatus* in its lower profile, less enlarged adapical pore-pairs and in its riblet ornamentation as opposed to the pitted ornamentation seen in *H. paucituberculatus* and *H. sphericus*. The vertical riblet ornamentation of *Noetlingaster?* sp. is characteristic of *Codiopsis* species such as *C. doma*, but *Noetlingaster?* sp. differs from *Codiopsis* in having no sharp reduction in the size of tubercles at the ambitus. It could possibly be the juvenile of a very much larger *Codiopsis* species, such as *C. stephensoni* Cooke, but it has open gonopores, which suggests that it is a genuinely small species. It differs from species such as *Codiopsis bruni* Lambert & Thièry (Maastrichtian of the Netherlands) and *C. disculus* Peron & Gauthier (late Campanian of Algeria, early Maastrichtian of Spain) in having a smooth, pustule-free upper surface. This specimen most likely represents a small *Noetlingaster*, one in which only the primary interambulacral tubercles have formed. However, neither of the named species of *Noetlingaster* shows the distinct vertical ribbing that characterises this specimen.

Order **PHYMOSOMATOIDA** Mortensen, 1904
Family **PHYMOSOMATIDAE** Pomel, 1883
Genus ***PHYMOSOMA*** Haime, *in* d'Archiac & Haime, 1853

Phymosoma hexoaporum Lambert, 1927   Pl. 13, figs
                                                                            1–3; Figs 32, 33

1908   *Phymosoma (Cyphosoma) Archiaci* Cott. var: Cottreau: 21, pl. 3, fig. 1.
1927   *Phymosoma hexoaporum* Lambert: 35, pl. 2, figs 25–27.
1933   *Phymosoma Paronai* Checchia-Rispoli: 11, pl. 2, figs 4–7.

MATERIAL. Nineteen specimens of which the biometric data was drawn from the following: BMNH EE3607–08, EE3610–12, EE3614, EE3616, EE3618, EE3941.

OCCURRENCE. This species is found almost exclusively in the lowest beds of the Simsima Formation at Jebel Buhays, section 1 (16), and the immediately adjacent Jebel Thanais (3). In addition one specimen was found loose in the scree in Jebel Rawdah, section 3, and another in Bed 2 at Jebel Rawdah, section 4. Cottreau (1908) recorded an identical specimen from the late Cretaceous (?Maastrichtian) of Marohita, Eastern Madagascar.

DIAGNOSIS. A *Phymosoma* with a single large primary interambulacral tubercle on all plates, and one or two small adradial tubercles. Plates are composed of six or seven elements at the ambitus and pore-pairs are biserial from about the ambitus adapically. Interradial zones of small granules are very well developed.

DESCRIPTION. Tests range from 23 to 50 mm in diameter and are circular in outline. The test is depressed in profile (Pl. 13, fig. 3), with a height that is 34–46% of the test diameter (mean = 42%, SD = 4·4%, N = 8: Fig. 32). The ambitus lies slightly below mid-height.

The apical disc is caducous and is missing from all specimens. The outline of the apical disc is pentagonal with angles pointing interradially and projecting slightly further into the posterior interambulacrum (Pl. 13, fig. 2).

Ambulacra taper slightly both adapically and adorally. They measure 22–26% of the test diameter in width at the ambitus. All plates are polygeminate (Fig. 33). Above the ambitus pore-pairs are biserial and plates are composed of six to eight elements. Plate compounding is in the phymosomatid style. At the ambitus the pore-pairs are in arcs of six or seven in specimens more than 25 mm diameter, while subambitally they are quinquegeminate. Immediately adjacent to the peristome there are a couple of quadrigeminate plates. There are no sphaeridial pits adorally. Each compound plate carries a single large imperforate, crenulate tubercle, as large as the adjacent interambulacral primary tubercles. This occupies most of the plate. However, perradially there is a narrow band of small secondary and miliary tubercles (Pl. 13, fig. 3). Primary tubercles more or less reach the apex. There are 57–58 pore-pairs in a column at 23–24 mm test diameter, rising to 138 at 50˙mm test diameter. Biserial pores appear immediately above the ambitus in most specimens and comprise 50–54% of the total number of pore-pairs in a column. In the very largest specimen, biserial pore-pairs extend to the subambital region.

Interambulacra are 32–38% of the test diameter in width at the ambitus. There are 10 plates in a column at 23 mm test diameter, rising to 18 at 50 mm test diameter (Fig. 32). Each plate carries a single large primary tubercle, centrally positioned. However, areoles are not contiguous, but are separated by a narrow band of miliary granules (Pl. 13, fig. 3). Tubercles are imperforate and crenulate and decrease in size gradually both adapically and adorally. There are one or two small secondary tubercles to each plate situated close to the adradial suture. In a few specimens these tubercles enlarge above the ambitus to about half the size of the primary tubercles, so as to form a secondary row. However, this is inconsistently developed. The interradius is broad and covered in scattered small secondary and miliary tubercles (Pl. 13, fig. 3). In some specimens (e.g. BMNH EE3614) this tuberculate band is relatively dense, whereas in other specimens (e.g. BMNH EE3618) tuberculation is more scattered. Both columns of plates reach the peristomial border.

The peristome is very slightly invaginated and occupies 40–47% of the test diameter. Buccal notches are small, but clearly incised (Pl. 13, fig. 1).

Lantern elements are seen scattered inside the test in BMNH EE3941. Hemipyramids are largely concealed by sediment, but one keeled tooth is seen in cross-section.

REMARKS. The variation encountered in the secondary tuberculation of this species is more marked than expected and is matched by a difference in the degree of tubercle crenulation. In the specimens with the denser miliary tuberculation interradially, there are usually well-developed secondary tubercles along the adradial margin in the region immediately above the ambitus, and primary tubercles are only weakly crenulate. In the more usual variety, the interradial zone has more scattered tuberculation, there is no enlarged secondary tuberculation and the primary tubercles have a well-developed and broad crenulate platform. These two forms may eventually prove to represent distinct species, but as they are both found at the same locality and the secondary tuberculation differences are not entirely consis-
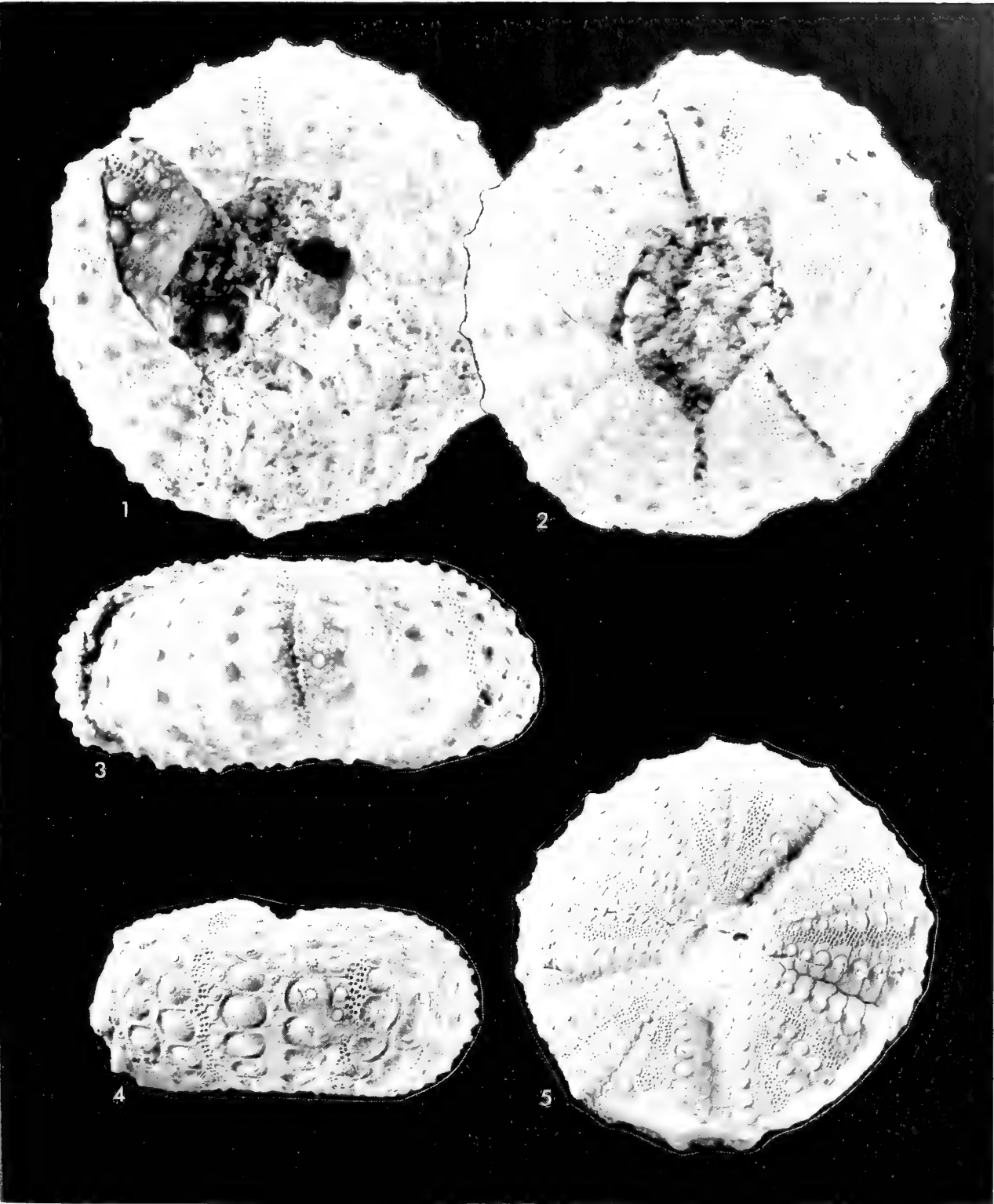
PLATE 13

Figs 1–3 *Phymosoma hexoaporum* Lambert. BMNH EE3614; **1**, oral; **2**, apical; **3**, lateral; all × 3. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation.

Figs 4, 5 *Actinophyma spectabile* Cotteau & Gauthier. B18731, Morgan Collection, Museum d'Histoire Naturelle, Paris; **4**, lateral; **5**, apical; both × 1·5. Senonian of Iran, no locality details.
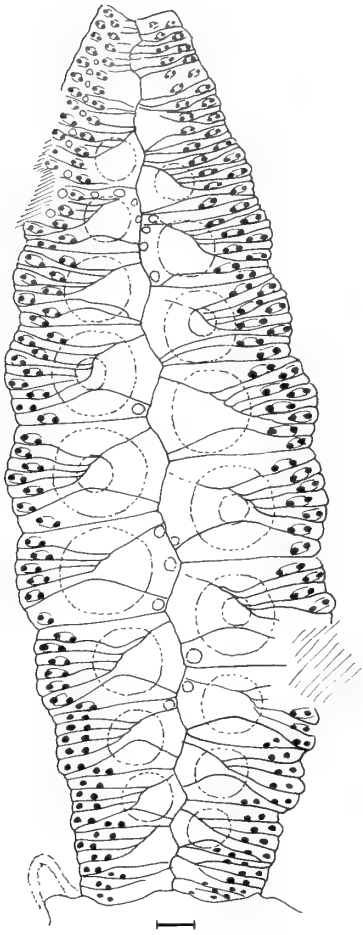
Fig. 33 Camera lucida drawing of ambulacral plating, from apex
(top) to peristomial margin (bottom), in *Phymosoma hexoaporum*
Lambert, BMNH EE3617. Scale bar = 1 mm.
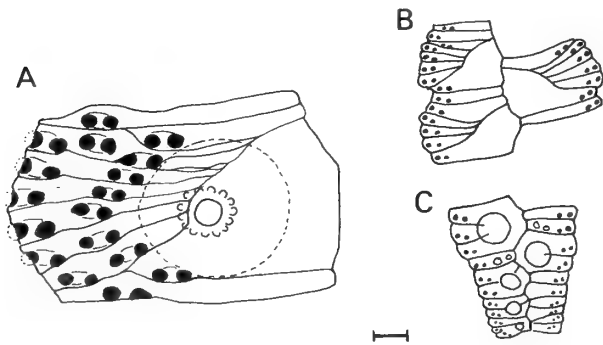
Fig. 34 Camera lucida drawings of plating in *Actinophyma
spectabile* Cotteau & Gauthier. **A**, adapical ambulacral plate from
a large individual, BMNH EE3599; **B**, supra-ambital ambulacral
plating in a juvenile, BMNH EE3601; **C**, adoral ambulacral
plating in a juvenile, BMNH EE3601. Scale bar = 1mm.

tent, the two forms are simply treated as varieties of the same
species here.
    The species described here appears identical to the speci-
men described from the Maastrichtian of Madagascar by

Cottreau (1908) under the name *Phymosoma archiaci* Cot-
teau var. It differs from true *P. archiaci* in having a broader,
more granular interradial zone, and in having less well-
developed secondary tubercles on interambulacral plates.
The species *P. hexoaporum* was established by Lambert
(1927) for specimens from the Maastrichtian of Sopeira,
province of Aragon, Spain. *P. hexoaporum* differed from all
other species of *Phymosoma* described previously in having
compound plates composed of six elements at the ambitus
rather than five. Later, Checchia-Rispoli (1933) described the
same species from the Maastrichtian of Libya under the name
P. paronai Checchia-Rispoli. This too has six or seven
elements in ambital ambulacral compound plates.

Genus *ACTINOPHYMA* Cotteau & Gauthier, 1895

Actinophyma spectabile Cotteau & Gauthier, 1895   Pl.
12, figs 4–7; Pl. 13, figs 4, 5; Fig. 34

1895   *Actinophyma spectabile* Cotteau & Gauthier: 98, pl.
            25, figs 6–10.
1895   *Cyphosoma persicum* Cotteau & Gauthier: 93, pl. 25,
            figs 3–4.
1902   *Actinophyma   spectabile   Cotteau   &   Gauthier*;
            Gauthier: 151, pl. 20, figs 7–10.
1935   *Actinophyma   spectabile   Cotteau   &   Gauthier*;
            Mortensen: 489, fig. 287.

TYPES. The holotype is the specimen described by Cotteau &
Gauthier from the upper Senonian of Endjir-kouh, Aftab
district, Iran.

MATERIAL STUDIED. Six specimens, BMNH EE3598–3603,
three of which are test fragments only. The following descrip-
tion is based on the two more or less complete specimens
BMNH EE3601 (a juvenile) and BMNH EE3603 (an adult).
Topotype material of *A. spectabile* in the Natural History
Museum and in the Morgan Collection, Museum d'Histoire
Naturelle, Paris, has been studied for comparison.

OCCURRENCE. Five of the specimens come from scree collec-
tions at Jebel Buhays, section 1 and are derived from the
lowest few metres of the Simsima Formation. Two other
specimens come from Jebel Rawdah section 3b, one from bed
8, the other from bed 9.
    The species range is 'Upper Senonian' of southern Iran and
Maastrichtian of the Oman Mountains.

DIAGNOSIS. A species of *Actinophyma* with strong radiating
ridges on the boss of primary tubercles. Ambulacra polyploid
adapically with up to 18 pore-pairs to an ambulacral plate
arranged irregularly.

DESCRIPTION. Tests range in diameter from 21·2 mm to
approximately 90 mm and are circular in outline. Test height
is 33 mm in the larger specimen and 9·4 mm in the smaller
(*ca.* 35–45% test diameter). In profile the ambitus is more or
less at mid-height and is smoothly rounded below and slightly
more conical above.
    The apical disc is small; 5·8 mm diameter in the 21 mm
individual (21% of test diameter) and probably only about 15
mm in the larger individual (16% of test diameter). Apical
disc plates are lost from all specimens and were evidently not
securely sutured to the corona. The opening is pentagonal in
outline (Pl. 12, fig. 4; Pl. 13, fig. 5).

Ambulacra are almost as broad as the interambulacra, being 25·3 mm wide at the ambitus in BMNH EE3603, as compared to the interambulacral width of 28·7 mm. Pore-pairs are in arcs of six on the oral surface, becoming biserial subambitally in the larger specimen and continuing so to the apex (Fig. 34A). Adapical plates have up to 18 pore-pairs, and show phymosomatid-style compounding (Fig. 34A). In the small individual adapical pore-pairs are only just begining to become biserial and all plates have just six or seven elements (Pl. 12, fig. 7; Fig. 34B). There are 10 or so plates in a column at 21 mm diameter and 18 or 19 at 90 mm diameter. Each plate carries a single large primary tubercle that occupies most of the plate. However, in the larger individual there is a narrow adradial band of heterogeneous small secondary and miliary tuberculation. Ambulacral tubercles are not contiguous, but are separated by a band of small secondary tubercles. Areoles are strongly sculptured by radial grooves that extend from the base towards the platform of the boss.

The adoral plating in the small individual (BMNH EE3601) is noteworthy, since it comprises simple plating arranged in triads (Fig. 34C). However, standard phymosomatoid-style compounding develops subambitally, and this appears to be simply a juvenile feature.

There are 11 interambulacral plates in a column at 21 mm test diameter, rising to about 18 at 90 mm test diameter. Each plate carries a large primary tubercle with a small imperforate mamelon and a crenulate platform. Areoles at the ambitus and adorally are confluent and are oval in outline. The areole bears strong radial grooves which extend up the sides of the boss (Pl. 12, figs 5, 6). These are most pronounced in the smaller individual. Tubercles decrease in size above the ambitus. The primary tubercles are centrally positioned on the plate and there are relatively broad adradial and interradial bands of secondary tuberculation. On plates around the ambitus there is an enlarged secondary tubercle to the adradial side of the primary tubercle, but otherwise secondary tuberculation is small and heterogeneous. The interradial zone is depressed and tubercle-free towards the apex.

The peristome is relatively small and invaginated. In the 21 mm individual it is 7·1 mm in diameter (33% of test diameter), and is proportionally smaller in the larger individual. Buccal notches are very shallow (Pl. 12, fig. 5).

REMARKS. When first erected (Cotteau & Gauthier, 1895), this species was based on a small individual 29 mm in diameter, which is virtually identical to BMNH EE3601 in morphology. In the same publication Cotteau & Gauthier (1895: 91) erected another species, *Cyphosoma persicum* on the basis of a larger, but fragmentary specimen from Derre-i-Chahr. Subsequently, with the collection of more material, Gauthier (1902) recognized that *A. spectabile* and *C. persicum* were simply different growth stages of the same species and synonymized the two, selecting *A. spectabile* as the valid name.

The characteristic radial striation, which is so strongly evident in juveniles, makes this an easily recognizable species. Only one other comparable species has been described, *Actinophyma* cf. *A. spectabile* Kier (1972: 68), from the Campanian of Saudi Arabia. This differs from the Iranian and Omani species in having deep pits developed at the corners of interambulacral plates on interradial sutures.
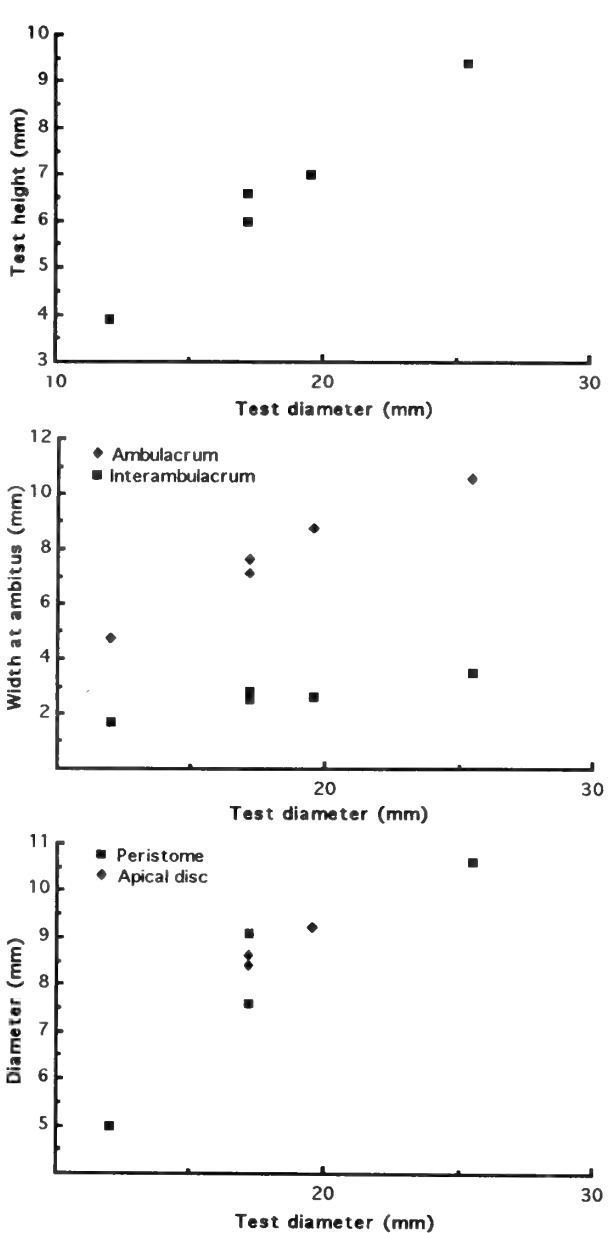
Fig. 35   Biometric data for *Plistophyma asiaticum* Cotteau & Gauthier.

Genus **PLISTOPHYMA** Peron & Gauthier, *in* Cotteau, Peron & Gauthier, 1881.

Plistophyma asiaticum Cotteau & Gauthier, 1895 Pl. 14, figs 1–7; Figs 35, 36

1895   *Plistophyma asiaticum* Cotteau & Gauthier: 105, pl. 16, figs 11–14.

TYPES. The holotype is the single specimen described and figured by Cotteau & Gauthier. It is not in the Morgan collection in the Museum d'Histoire Naturelle, Paris.

MATERIAL STUDIED. Six specimens, BMNH EE3572–76, EE4932. Only BMNH EE3573, which is incomplete, was

omitted from the biometric analysis given below.

OCCURRENCE. In the western Oman Mountains this species was found at the following levels and localities:

Jebel Buhays, section 1: loose in scree, derived from lowest few metres of the Simsima Formation (4).

Jebel Thanais: From the lowest metre of Simsima Formation (2).

Jebel Rawdah, section 2, bed 4 (1).

The species was described from the Senonian of Derre-i-Chahr, southern Iran and there are no other records.

DIAGNOSIS. A *Plistophyma* in which the ambital interambulacral plates are very much smaller and narrower than either adoral or adapical plates.

DESCRIPTION. Tests range in diameter from 12 to 25·5 mm and are rounded pentagonal in outline with the angles interradial. Tests are depressed and rounded in profile, with the ambitus at or very slightly below mid-height (Pl. 14, figs 3, 4). Test height is 33–38% of test diameter (mean = 36%).

The apical disc is large and pentagonal in outline with the angles interradial (Pl. 14, fig. 2). It is 47–50% of the test diameter in diameter and is not invaginated. No specimen retains any apical disc plates but, to judge from the size and shape of the opening, disc plating was presumably monocyclic.

Ambulacra are 13–16% of the test diameter in width at the ambitus. They are narrowest ambitally and expand slightly adapically (Fig. 36A). Plates both at the ambitus and adorally are trigeminate with all three elements reaching the perradial suture (Fig. 36C). The central element is the largest. Each plate carries a single imperforate, non-crenulate tubercle which straddles all three elements. Adorally, pore-pairs become crowded so as to form small phyllodes (Pl. 14, fig. 6). Immediately above the ambitus pore-pairs become biserially arranged and primary tubercles diminish in size and do not reach the apex (Pl. 14, fig. 5). There are 48 pore-pairs in a column (of which the most adapical 18–20 are biserially arranged). There are 12 or 13 primary tubercles. Secondary tubercles lie immediately adjacent to each pore-pair and may also occur along the perradius on occasional elements.

Interambulacra are 39–44% of the test diameter in width at the ambitus. Each plate is very wide and short and bears a row of small, equal-sized tubercles. These are imperforate and appear non-crenulate, but on close inspection of well-preserved material (e.g. BMNH EE3573) there are faint traces of crenulation to larger tubercles. At the ambitus the interambulacral plates become very much narrower and the size of the tubercles more or less halves (Pl. 14, figs 3, 4; Fig. 36B). All plates are arranged to form a pronounced downward-pointing V. Both columns of plates reach the peristomial border. The peristome is 42–52% of the test diameter in diameter and is hardly invaginated. There are very feeble buccal notches. The perignathic girdle consists of small auricles which do not meet above the perradius.

REMARKS. The species is distinguished from the type species *P. africanum* Peron & Gauthier (Cotteau *et al.* 1881) by its somewhat sharper decrease in interambulacral plate size at the ambitus. However, the two species are very similar indeed in other features and the Algerian and Omani-Iranian species may eventually turn out to be conspecific. The residual crenulation on well-preserved tubercles and the large
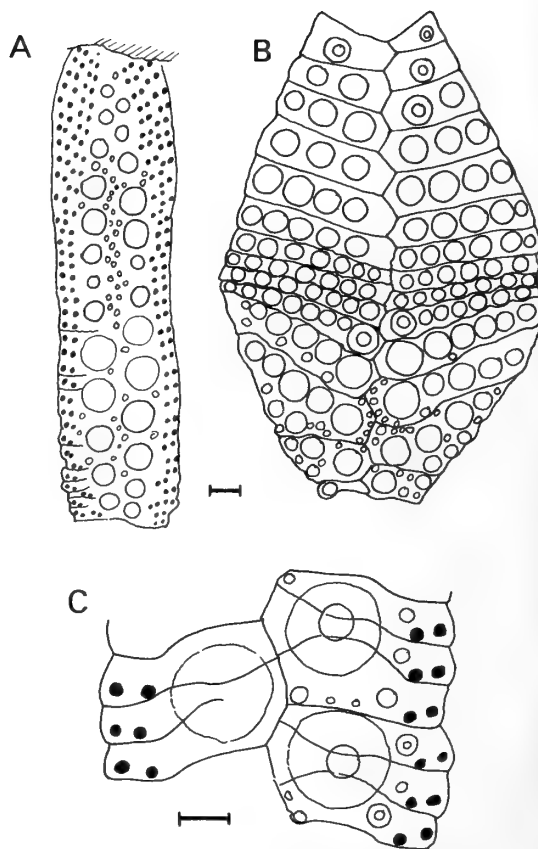
Fig. 36 Camera lucida drawings of plating in *Plistophyma asiaticum* Cotteau & Gauthier, BMNH EE3575. **A**, ambulacrum, from apex (top) to peristomial margin (bottom); **B**, interambulacrum from apex (top) to peristomial margin (bottom); **C**, detail af ambital ambulacral plating. Scale bars = 1 mm.
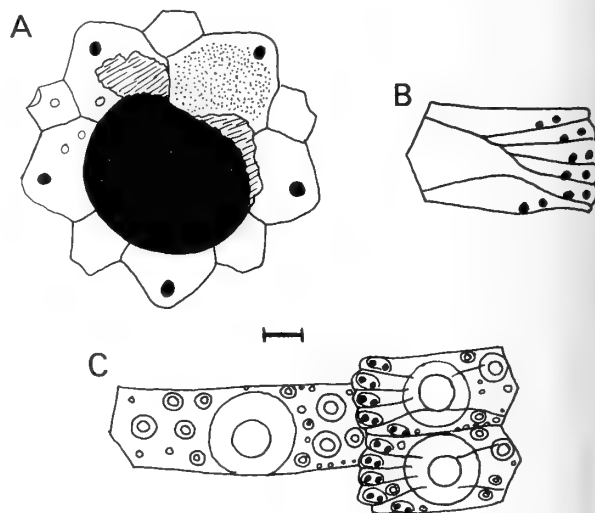
Fig. 37 Camera lucida drawings of plating in *Circopeltis? emiratus* sp. nov. **A**, apical disc, BMNH EE3584; **B** ambital ambulacral plating, BMNH EE3582; **C**, ambital plating, ambulacrum to right, interambulacral plate to left, BMNH EE3584. Scale bar = 1 mm.
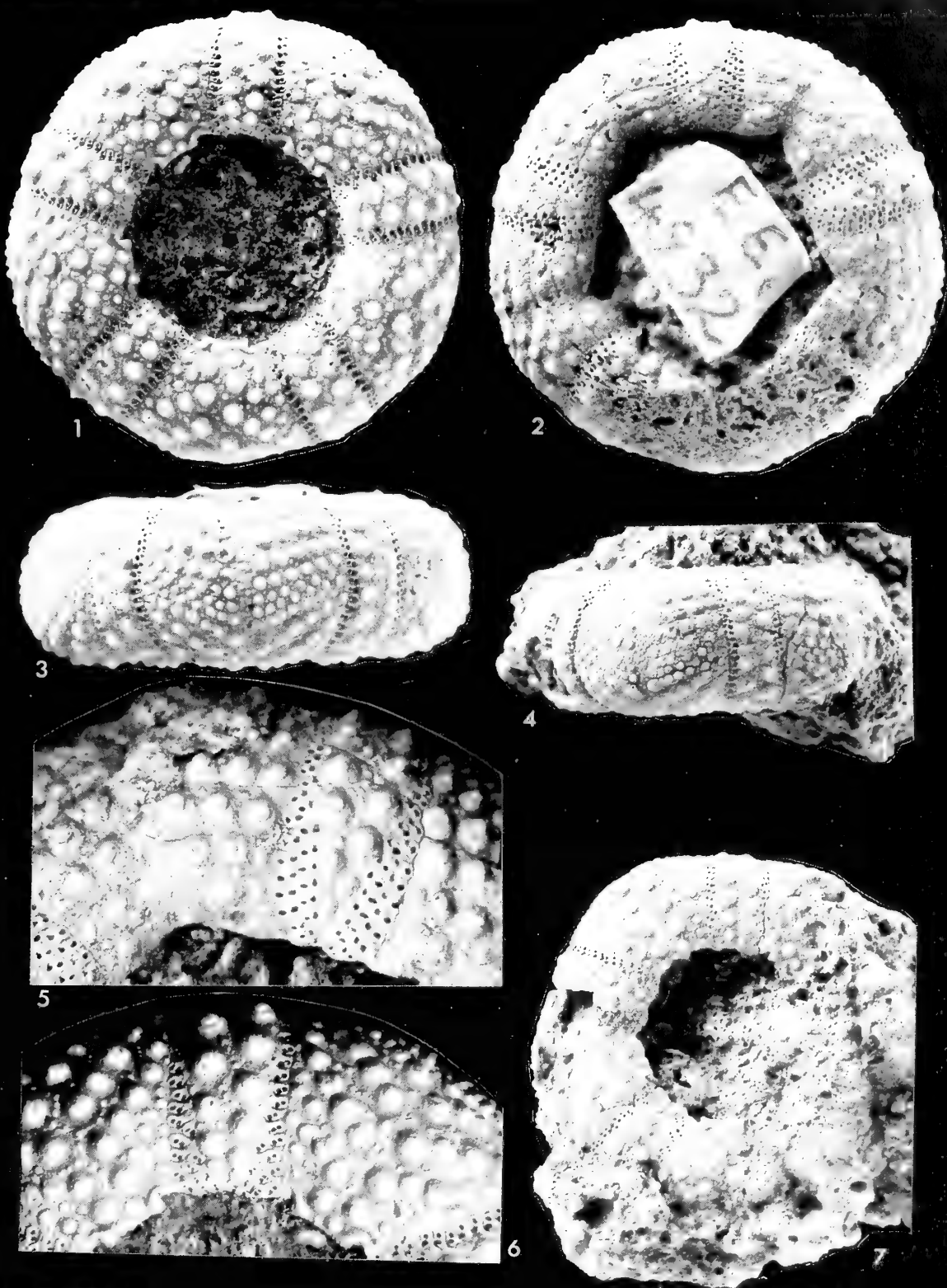
PLATE 14

Figs 1–7   *Plistophyma asiaticum* Cotteau & Gauthier. **1–3, 6**, BMNH EE4932; **1**, oral, × 5; **2**, apical, × 5; **3**, lateral, × 5; **6**, detail of peristomial region, × 8. Jebel Thanais, lowest 1 m of the Simsima Formation. **4, 7**, BMNH EE3575; **4**, lateral; **7**, oral; both × 3. Jebel Thanais, basal 1 m of the Simsima Formation. **5**, BMNH EE3572; apical detail, × 8. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation.

pentagonal caducous apical disc suggests that *Plistophyma* belongs within the phymosomatoids.

Family **STOMECHINIDAE** Pomel, 1883
Genus *CIRCOPELTIS* Pomel, 1883

Circopeltis? emiratus sp. nov.   Pl. 15, figs 1–3; Pl. 17, figs 1, 2; Fig. 37

TYPES. The holotype is BMNH EE3584 and paratypes are BMNH EE3582, EE3583, EE3585 and EE3596.

OTHER MATERIAL. There is one other fragment tentatively attributed to this species, BMNH EE3586.

OCCURRENCE. In the western Oman mountains this species is found at the following levels:
Jebel Buhays section 1: loose in scree (derived from lower beds of the Simsima Formation) (1).
Jebel Buhays section 3: immediately overlying prominent red marly sand level (*ca*. 3 m above the base of the Simsima Formation) (2).
Jebel Rawdah section 3: bed 6 (1). Section 3b basal 1 m (1).
Jebel Rawdah, section 4: bed 4 (1).

It is thus known from the Maastrichtian of the western Oman Mountains.

DIAGNOSIS. Test low, domal; apical disc hemicyclic with plates firmly bound to the corona. Ambulacra straight, plating compound in the phymosomatoid style with five or six elements to a compound plate; pore-pairs arranged in arcs from apex to peristome. There is a single large primary tubercle to each plate with broad adradial and interradial zones of secondary tuberculation.

DESCRIPTION. Tests range in diameter from 20·1 mm to 47·2 mm and in height from 11·8 to 23·5 mm (mean test height is 53% of test diameter). The test is circular in outline and flattened ovate in profile, with the ambitus at approximately 40% of test height above the base.

The apical disc is hemicyclic, with the three anterior oculars insert and the posterior two exsert (Fig. 37A). The apical disc is 19–24% of the test diameter in diameter (mean = 22%) and the periproct occupies approximately 55% of the apical disc diameter. The periproct is D-shaped in outline, with the slightly flattened edge abutting the madreporite. Genital plate 2 is the largest and is tumid and covered in dense madrepores. Other genital plates and all ocular plates have a scattering of small miliary tubercles.

The ambulacra are 22–24% of the test diameter in width at the ambitus. They are straight and taper gradually adapically. All plates are compound in the phymosomatid style (Fig. 37B) and most are composed of five, or occasionally six, elements. The three most adoral plates however are composed of just four elements. Pore-pairs are arranged in arcs and phyllodes are developed around the peristomial edge. Each compound plate has a single large primary tubercle (imperforate and non-crenulate) that overlaps all five (or six) elements that make up the compound plate (Fig. 37C; Pl. 17, fig. 1). There is a much smaller secondary tubercle lying perradially, plus one or two scattered miliary granules. The perradial zone is relatively broad. There are 14 compound plates and 73 pore-pairs at 20 mm test diameter, rising to 18

compound plates and 88 pore-pairs at 37 mm test diameter. There are no sphaeridial pits.

Interambulacra are broad and carry two rows of primary tubercles, set close to the adradial margin. There are 13 plates in a column at 20 mm test diameter, rising to 17 at 37 mm test diameter. Areoles are almost contiguous adorally but are separated adapically. The mamelon is large and imperforate and there is a narrow ledge that may retain faint traces of crenulation in well-preserved individuals. Adradially there is a narrow band of small secondary tubercles and miliary granules. Interradially the plates are slightly depressed and there are small and irregularly scattered secondary tubercles throughout (Pl. 17, fig. 2). Both columns reach the peristomial margin.

The peristome is about 42% of the test diameter across. It is slightly invaginated. Buccal notches are moderately well-developed and have a thickened lip. Lantern and spines are unknown.

REMARKS. This species has a phymosomatid style of ambulacral compounding. However, the apical disc structure differentiates it from the great majority of phymosomatids, since these almost all have monocyclic apical discs that are typically caducous. Only *Glyptocidaris* has a comparable apical disc. Furthermore, this species has tuberculation that is virtually non-crenulate, whereas other genera, including *Glyptocidaris*, show stronger crenulation. The species is here tentatively assigned to the genus *Circopeltis*. *Circopeltis* has polygeminate plate compounding and a hemicyclic apical disc. *Circopeltis* also has non-crenulate tuberculation. However, its ambulacral compounding style is unreported and it is not yet known whether it is phymosomatoid.

It differs from *Phymechinus? perplexus* in its finer tuberculation, with more extensive scattered secondary tuberculation. More importantly it has ambulacral pore-pairs in simple arcs throughout. In *Phymechinus* pore-pairs become irregularly biserial adapically. Furthermore, *Circopeltis?* has a larger peristome and much less well developed phyllodes than does *Phymechinus? perplexus* from the same levels. However, there is little doubt that the two forms are rather closely related.

Genus *PHYMECHINUS* Desor, 1856

Phymechinus? perplexus sp. nov   Pl. 15, figs 4–10; Figs 38, 39

TYPES. Holotype EE3579, paratypes BMNH EE3581, EE3591, EE3593, EE3619.

MATERIAL STUDIED. 14 specimens, of which biometric data was derived from the following: BMNH EE3578–79, EE3581, EE3989, EE3991–94, EE3619.

OCCURRENCE. All specimens come from Jebel Rawdah as follows:
Section 1: bed 4 (2).
Section 2: bed 6 (2); bed 8 (4); bed 11 (1); loose in scree (4).
Section 4: bed 8/9 (1).

DIAGNOSIS. Apical disc small, caducous. Ambulacra polygeminate with seven or eight elements to a compound plate. Plate compounding phymosomatid-style. Pore-pairs arcuate or irrgularly multiple above. One primary imperforate, crenulate tubercle on each ambulacral and interambu-
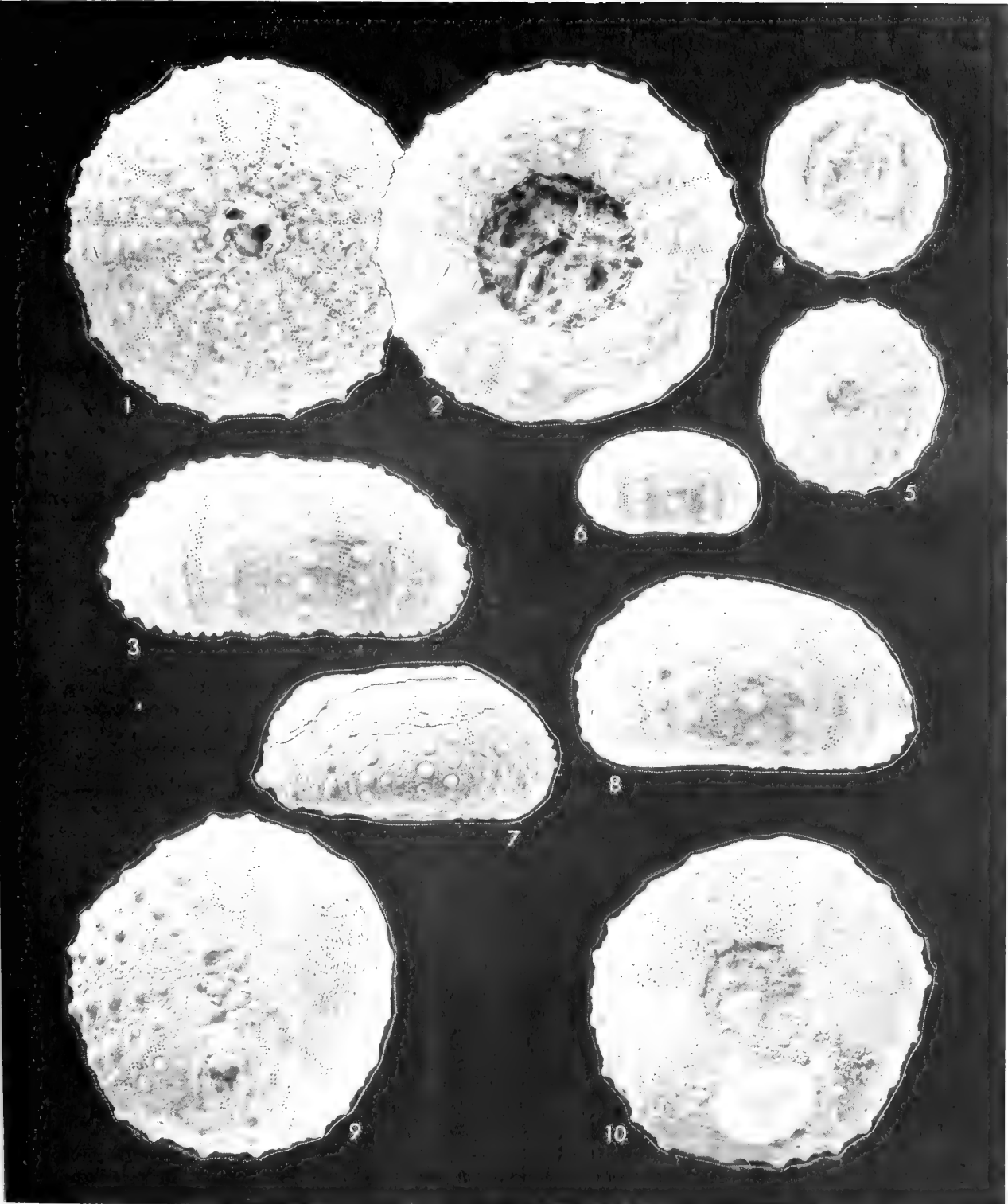
Figs 1–3 *Circopeltis? emiratus* sp. nov. BMNH EE3584, holotype; **1**, apical; **2**, oral; **3**, lateral; all × 2. Jebel Buhays, section 3, *ca.* 3 m above the base of the Simsima Formation.
Figs 4–10 *Phymechinus? perplexus* sp. nov. **4–6**, BMNH EE3591, paratype; **4**, oral; **5**, apical; **6**, lateral; all × 2. Jebel Rawdah, section 2, bed 8. **7**, BMNH EE3579, holotype; lateral, × 1. Jebel Rawdah, section 2, bed 8. **8–10**, BMNH EE3581, paratype; **8**, lateral; **9**, apical; **10**, oral; all × 2. Jebel Rawdah, section 2, loose in scree derived from beds 3–10.
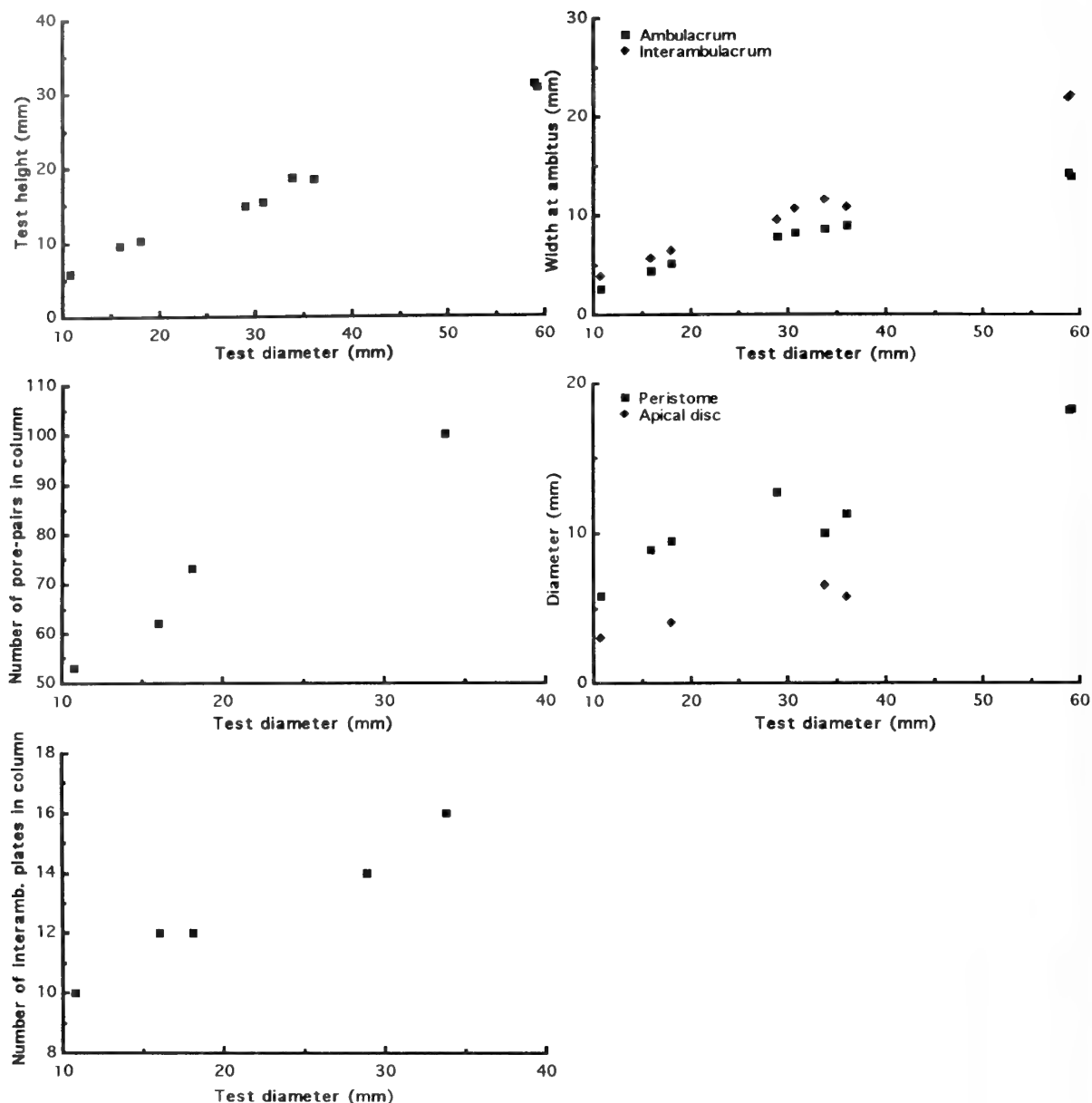
Fig. 38 Biometric data for *Phymechinus? perplexus* sp. nov.

lacral plate. Mamelons very large and crenulation feebly developed. Lower surface flat, peristome small with feeble buccal notches. Phyllodes extremely well-developed.

DESCRIPTION. Tests are 11 to 60 mm in diameter and 5·8 to 31·2 mm in height (test height 50–60% of diameter; mean = 54%, SD = 3·2%, N = 9). They are circular in outline and bun-shaped in profile, with a broad base and depressed conical upper surface (Pl. 15, fig. 8). The ambitus lies at approximately 30% of test height above the base.

The apical disc is small and circular, only 16–28% of the test diameter across (Pl. 15, fig. 9). It is proportionally smaller in larger individuals (Fig. 38). No specimen retains any apical disc plating, but to judge from the small size of the

opening, plating is almost certain to have been dicyclic or hemicyclic.

Ambulacra are only slightly narrower than interambulacra at the ambitus and measure 23–28% of the test diameter in width (mean = 25·5%, SD = 1·8%, N = 9). They are more or less straight, tapering slightly adorally and more significantly adapically. All plates are polygeminate with seven (rarely six or eight) pore-pairs to an ambital plate. Plate compounding is in the phymosomatid style (Figs 39A, B). Pore-pairs are strongly arced at the ambitus, but tend to become irregularly biserial or pleuriserial adapically and adorally (Figs 38C, D). Close to the apex, pore-pairs once again become uniserially arranged. Adapically, small secondary tubercles occur scattered within the pore zone. However,

there are a few specimens (e.g. EE3581) in which the pore-pairs are in uniserial arcs right to the apex. Each plate carries a single large primary tubercle that occupies most of the plate (Pl. 15, fig. 7; Figs 38A, B). This has a relatively well-developed imperforate mamelon and is distinctly crenulate, though the surrounding platform is not very broad. Areoles are circular and separated by a single ring of small secondary and miliary tubercles. There are 53 pore-pairs in a column at 11 mm test diameter, rising to about 100 pore-pairs at 34 mm test diameter (Fig. 38). Tubercles are largest at the ambitus and decrease in size gradually both adapically and adorally. Adorally there are very strong phyllodes composed of circular pore-pairs with well-developed periporal muscle attachment areas (Pl. 15, fig. 10). These phyllodes are so large as to make up more than half of the ambulacral width.

Interambulacra are relatively narrow, being only 30–37% of the test diameter in width at the ambitus. There are 10 plates in a column at 11 mm test diameter, rising to 16 at 34 mm test diameter. Each plate carries a large primary tubercle which is imperforate and weakly crenulate. In smaller specimens (i.e. less than 35 mm) these are the only large tubercles present, although a distinct small secondary tubercle is present both adradially and interradially. In specimens around 58 mm test diameter the adradial secondary tubercle reaches approximately half the diameter of the primary tubercle at the ambitus and adorally, and there are additional smaller secondary tubercles close to the adradial suture. Primary and secondary tubercles extend to the apex and peristome. The primary tubercles are non-confluent, being separated by a single row of miliaries.

The peristome is 30–55% of the test diameter in width (proportionally smaller in larger individuals) and is hardly invaginated, the entire lower surface being flat. Buccal notches are small and poorly developed. Spines, lantern and pedicellariae are all unknown.

REMARKS. It is with some slight hesitation that I refer the new species *P? perplexus* to this genus. This species has stout tubercles with large mamelons and virtually no platform. Nevertheless fine crenulation is developed around the mamelon, though it is often difficult to see unless preservation is near perfect. The ambulacral plate compounding is phymosomatid in style, with adapical pore-pairs either strongly arcuate or, more often, actually multiple in an irregular way. The apical disc is small and unlikely to be monocyclic, but plating is not preserved. The type species of *Phymechinus*, *P. mirabilis* (Agassiz) comes from the Middle Oxfordian and has a similar overall shape, small apical disc and stout tuberculation. Well-preserved specimens (e.g. Hess 1975, pl. 37, fig. 5) apparently show feeble crenulation. Unfortunately, none of the specimens I have examined show the style of ambulacral compounding. *P? perplexus* differs from the type species in having a proportionally smaller peristome and better developed phyllodes. It also has much less well-developed buccal notches. In tuberculation style it is very similar to Schluter's species *Phymechinus cretaceus* from the *B. mucronata* Zone, Upper Campanian of Ciply, Belgium, but this species has a much larger peristome and much less well-developed phyllodes. This species is easily distinguished from *Phymosoma* cf. *paroni* Checchia-Rispoli by its very much smaller apical disc, more subconical profile and compound amulacral plates that incorporate more than five elements. It is also easily distinguished from *Actinophyma*. Although *Actinophyma* has a similar arrangement of pore-pairs adapically, forming rather irregular multiple columns with interspersed tubercles, it is very different adorally. The peristome in *Actinophyma* is invaginated and the pore-pairs remain uniserial and rather widely spaced across the entire oral surface. In *P? perplexus* the pore-pairs form a very strong phyllode and the oral area is broad and flat.

It is distinguished from *Circopeltis emiratus* by its very much coarser tuberculation, smaller peristome, more polygeminate ambulacral compounding and cadoucous apical disc. Furthermore, *C. emiratus* never developed biserial pore-pairs adapically.

Genus *ECHINOTIARA* Pomel, 1883

Echinotiara perebaskinei Lambert, 1930   Pl. 16, figs 1–6; Pl. 17, figs 3, 6, 7; Figs 40, 41

1930 *Echinotiara perebaskinei* Lambert, in Lambert & Perebaskine: 472, pl. 38, figs 1–5.

TYPES. The two specimens figured and described by Lambert and presumably in the Lambert Collection, Université de Paris VI, France.

MATERIAL STUDIED. 82 specimens of which only the following were used in the biometric analysis: BMNH EE3756–57, EE3761–63, EE3767–69, EE3772, EE3774, EE3782, EE3785–88.

OCCURRENCE. Along the western margins of the Oman mountains this species is confined to the lowest arenaceous levels of the Simsima Formation at Jebel Rawdah. It occurs as follows:
Jebel Rawdah, section 2: bed 4 (6); bed 6 (9); bed 8 (49); bed 11 (3); loose in lower scree (17).
Jebel Rawdah, section 3b: bed 3 (1).
Jebel Rawdah, section 4: bed 2 (1); bed 8/9 (1).

The species was originally described from the 'Calcaires inferieur a *Libycoceras*, Maastrichtien' at Oued Tarinkat, Tchi-Dermine and Oued Tinamassine in the district of Gao,
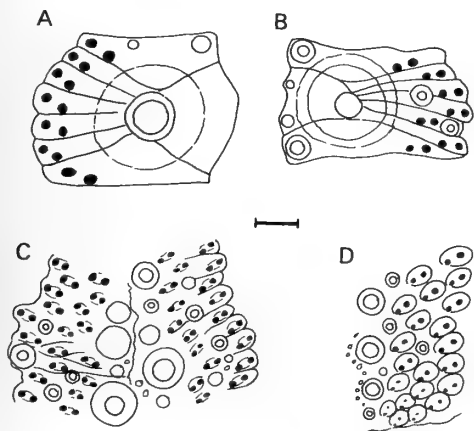
Fig. 39 Camera lucida drawings of plating in *Phymechinus? perplexus* sp. nov., BMNH EE3581. **A,** ambital ambulacral plate; **B,** adapical ambulacral plate; **C,** adapical pore-pair arrangement; **D,** adoral pore-pair arrangement. Scale bar = 1 mm.
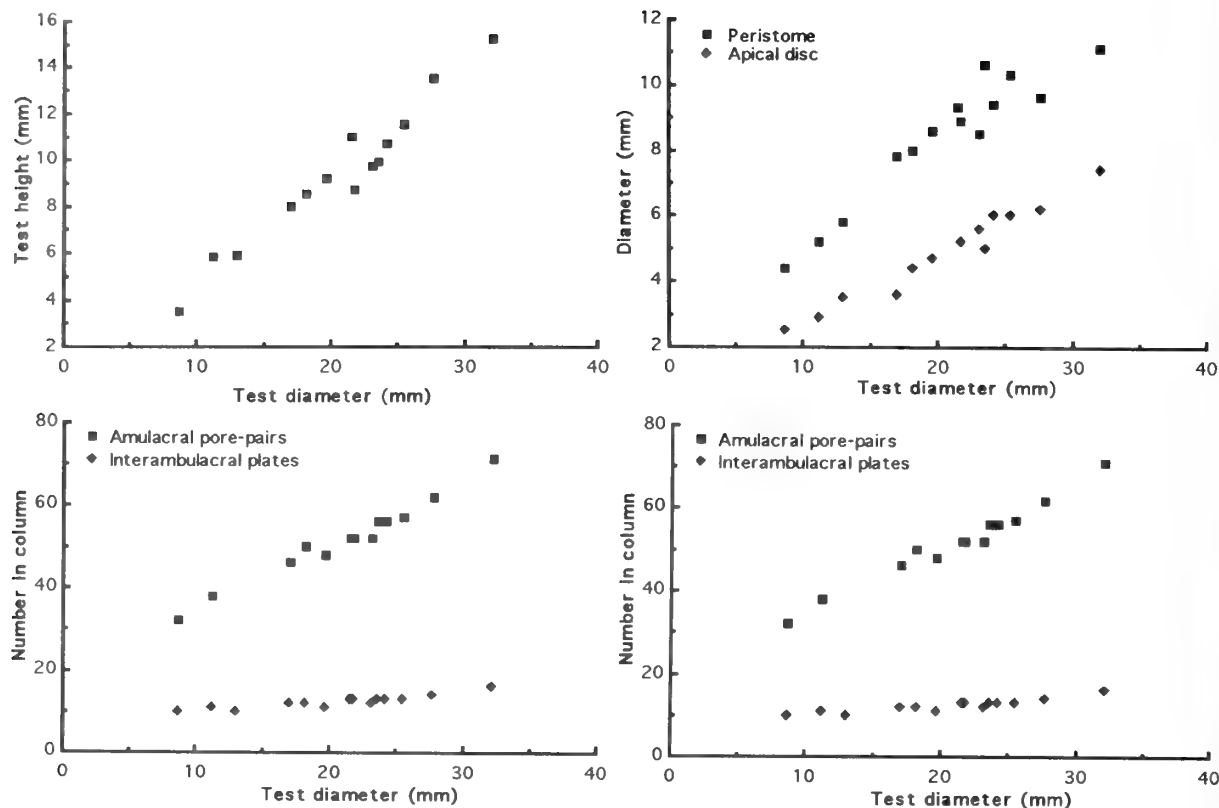
Fig. 40 Biometric data for *Echinotiara perebaskinei* Lambert.

Niger (Lambert & Perebaskine 1930). Amard *et al.* (1981: 124) reported an *Echinotiara* cf. *perebaskinei* Lambert from the Upper Maastrichtian of Tademait, Algeria, but as no figures or description are given it is not possible to confirm this record.

DIAGNOSIS. An *Echinotiara* with a relatively small caducous apical disc, ambulacral pore-pairs in arcs of three, with very strong phyllodes developed adorally. Interambulacral plates with a single large primary tubercle and well-developed adradial and interradial secondary tubercles that diminish in size adapically.

DESCRIPTION. Tests range from 9 to 32 mm in diameter and are more or less circular in outline. Test height is 40–52% of test diameter (mean = 46%, SD = 3·7%, N = 14). In profile the test is low conical (Pl. 16, fig. 3), with the ambitus approximately 40% above the base.

The apical disc is always missing and plating can only have been loosely fixed to the corona. The apical disc outline is irregularly circular (Pl. 16, fig. 1) and is 21–29% of the test diameter in length (mean = 24%, SD = 2·1%, N = 13). To judge from the size, it must have been dicyclic or hemicyclic.

Ambulacra are trigeminate throughout with pore-pairs arranged in distinct arcs of three (Fig. 41A). Ambulacra are relatively broad, being approximatley 22% of the test diameter in width at the ambitus. They taper gradually adapically, but primary tubercles continue to the apex (Pl. 17, fig. 3). Adorally the ambulacra remain broad and there are large, well-developed phyllodes, which in specimens 25 mm in diameter include at least 22 pore-pairs in each column (Pl. 16,

fig. 5). Each compound plate carries a single large imperforate and non-crenulate tubercle that overlaps all three elements (Fig. 41). Plate compounding is diadematoid in style, with all three elements reaching the perradius and the middle plate pinched towards the centre of the plate (Fig. 41C). The lowest element in each compound plate carries a small secondary tubercle adradially and perradially. There are 32 pore-pairs in a column at 9 mm test diameter, rising to 71 at 32 mm test diameter (Fig. 40).

At the ambitus the interambulacra are 35–38% of the test diameter in width. Both columns reach the peristomial border, although the interambulacra taper considerably towards the peristome. Plates at the ambitus are longer than wide and are slightly curved. Each plate carries a single large imperforate and apparently non-crenulate tubercle at its centre (Pl. 17, fig. 7). The mamelon is slightly undercut but there is little surrounding platform developed. On the adradial side there are one or two smaller secondary tubercles, while on the interradial edge there is a single secondary tubercle (Fig. 41C). These primary and secondary tubercles are relatively coarse and occupy most of the available space. There are, however, miliary granules and small tertiary tubercles along the adapical margin and in spaces adjacent to the primary tubercle. There are 10 plates in a column at 9 mm test diameter, rising to 16 at 32 mm test diameter. Primary tubercles continue to the apex and there is no median naked zone.

The peristome is circular and measures 35–50% of the test diameter in diameter (it is proportionally larger in smaller individuals (Pl. 16, figs 4, 5). It is only slightly sunken and
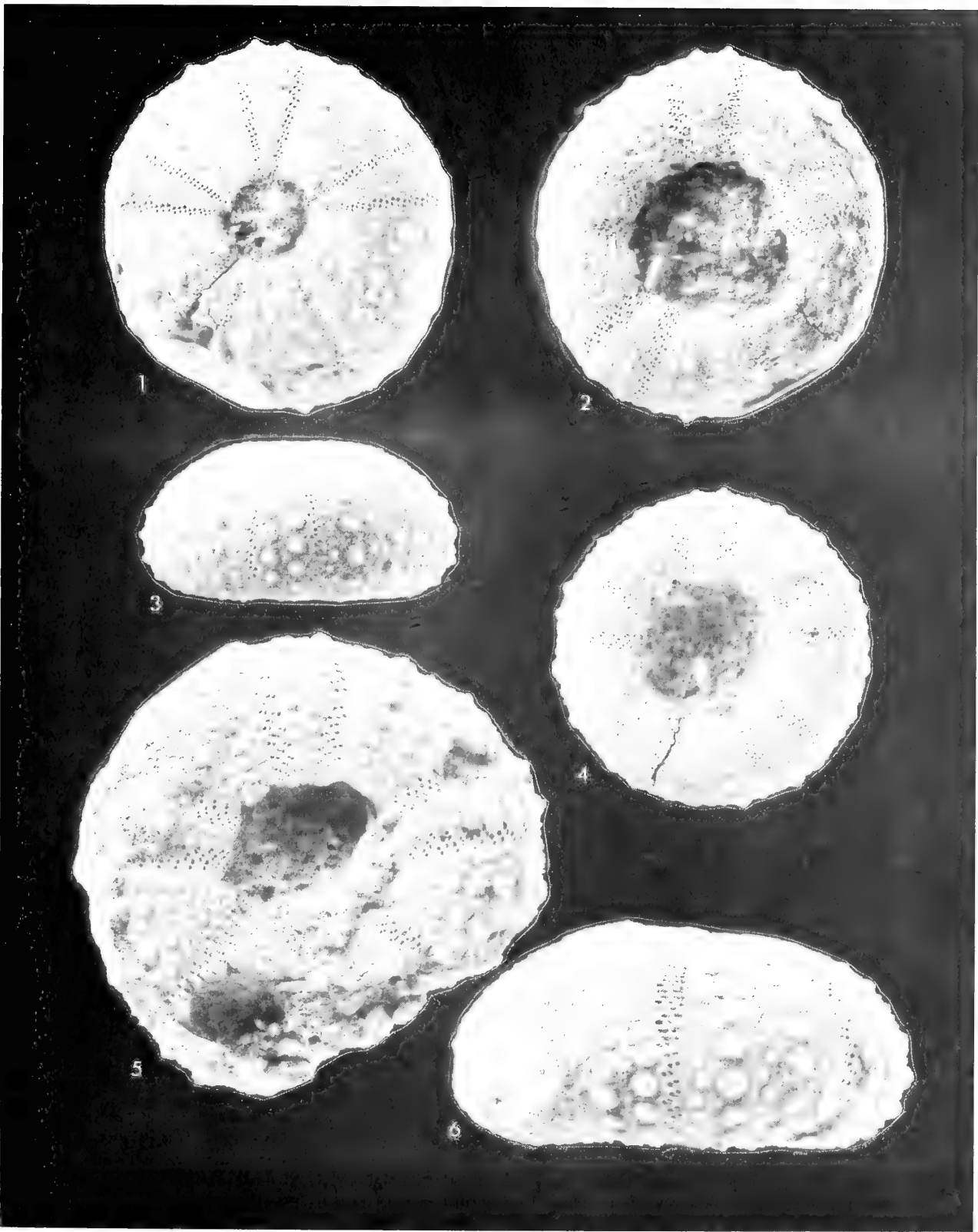
PLATE 16

Figs 1–6 *Echinotiara perebaskinei* Lambert. Jebel Rawdah, section 2, beds 6–8. **1, 2**, BMNH EE3756; **1**, apical, **2**, oral; both × 3. **3, 4**, BMNH EE3768; **3**, lateral; **4**, oral; both × 3. **5, 6**, BMNH EE3788; **5**, oral; **6**, lateral; both × 3.
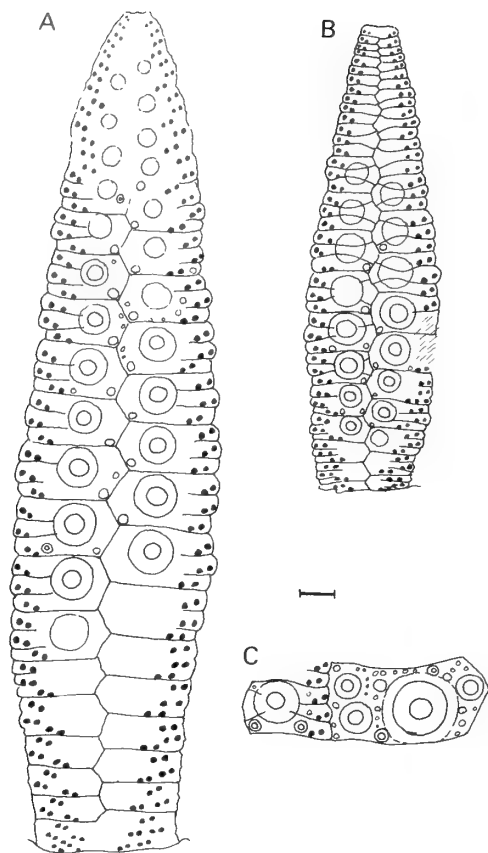
Fig. 41 Camera lucida drawings of plating in *Echinotiara perebaskinei* Lambert. **A**, BMNH EE3769, ambulacrum from apex (top) to peristome margin (bottom); **B**, BMNH EE3763, ambulacrum from apex (top) to peristome margin (bottom); **C**, ambital ambulacral and interambulacral plate, BMNH EE3763. Scale bar = 1 mm.

buccal notches are small but distinct.

The perignathic girdle structure is seen in BMNH EE3783 and EE3788. It consists of two long peg-like auricles that do not meet above the perradius. Spines and lantern are unknown.

REMARKS. This species lacks crenulate tuberculation, although preservation is usually inadequate to be certain for most specimens. It could easily be mistaken for *Orthopsis miliaris* on account of its very similar tuberculation and test shape. However, *Orthopsis* has perforate tuberculation and its ambulacral pore-pairs are strictly uniserial, not arranged in arcs of three as in *Echinotiara*. Furthermore, *Echinotiara* has well-developed phyllodes that are never seen in *Orthopsis*.

The type material described and illustrated by Lambert differs in apparently having slightly less well developed phyllodes adorally at comparable sizes, but for the present the two populations are treated as conspecific.

Cohort **IRREGULARIA** Latreille, 1825
Order **HOLECTYPOIDA** Duncan, 1889
Family **HOLECTYPIDAE** Lambert, 1899
Genus *COENHOLECTYPUS* Pomel, 1883

Coenholectypus inflatus (Cotteau & Gauthier, 1895)
Pl. 18, figs 7–11; Figs 42, 43A, C

1895   *Holectypus inflatus* Cotteau & Gauthier: 73, pl. 12, figs 1–4.
?1989   *Holectypus (Caenholectypus) inflatus* Cotteau & Gauthier; Ali: 401, fig. 4 (1).

TYPES. The specimen described and illustrated by Cotteau & Gauthier, from the late Cretaceous of Aftab, southern Iran.

MATERIAL STUDIED. Thirty specimens, of which 16 were used in the biometric analysis (BMNH E82644, EE3399, EE3401–04, EE3406–07, EE3409, EE3411–15, EE3417, EE3429).

OCCURRENCE. There are two morphologies found along the western foothills of the Oman Mountains:

Depressed variety: this occurs at Jebel Huwayyah, from an uncertain horizon. It is also found at Jebel Buhays (sections 1 and 2) in the lowest limestones. It is more common at Jebel Rawdah: in section 3 it occurs reasonably abundantly in bed 6 (6) and is found at a comparable level in section 4 (beds 19 and 21–22 and at top of measured section) (10). It also occurs frequently at and immediately above the level of the first major red parting in section 3 (bed 5).

More inflated, rounded forms are recorded from Jebel Huwayyah (unknown horizon); and from Jebel Rawdah, Section 2, bed 6, section 3, bed 10, section 4, bed 13.

DESCRIPTION. Tests are circular in outline and range from around 13 mm up to 56 mm in diameter. In profile their height varies from low conical to almost subglobular. Test height is 47–77% of test length (Fig. 42). The ambitus is well rounded and lies a little below midheight (Pl. 18, fig. 11).

The apical disc is small and compact with five gonopores. Genital plates are small and pentagonal and separated from one another by ocular plates that are almost as large (Fig. 43C). Madrepores occupy the entire central region.

Ambulacra are simple and uniserial, except adapically in larger specimens (40 mm diameter plus), where pore-pairs become slightly offset creating an incipient biserial arrangement. There is no pore crowding towards the peristome (Fig. 43A) and all plating is simple. Only close to the peristome does ambulacral plating become differentiated into triads with every third plate becoming enlarged. All pore-pairs are nonconjugate. There are approximately 100 pore-pairs in a column at 18 mm test length, rising to 185 at 56 mm test length (Fig. 42).

Interambulacra are standard in their structure. The periproct is oval in outline and lies close to the peristome and well separated from the ambitus (Pl. 18, fig. 7; Fig. 43A). It opens between interambulacral plates 2a,b and 6b,7a or 7a,b. Its width is 55–81% of its length (mean = 65%, SD = 7%, N = 17). The distance separating the periproct and peristome is small, only 20–50% of the periproct length; whereas the distance separating the periproct from the ambitus is much greater, being 110–260% of the periproct length (greatest in largest individuals).

The peristome is circular with feeble buccal notches. It is 15–35% of test length in diameter (mean = 23%, SD =
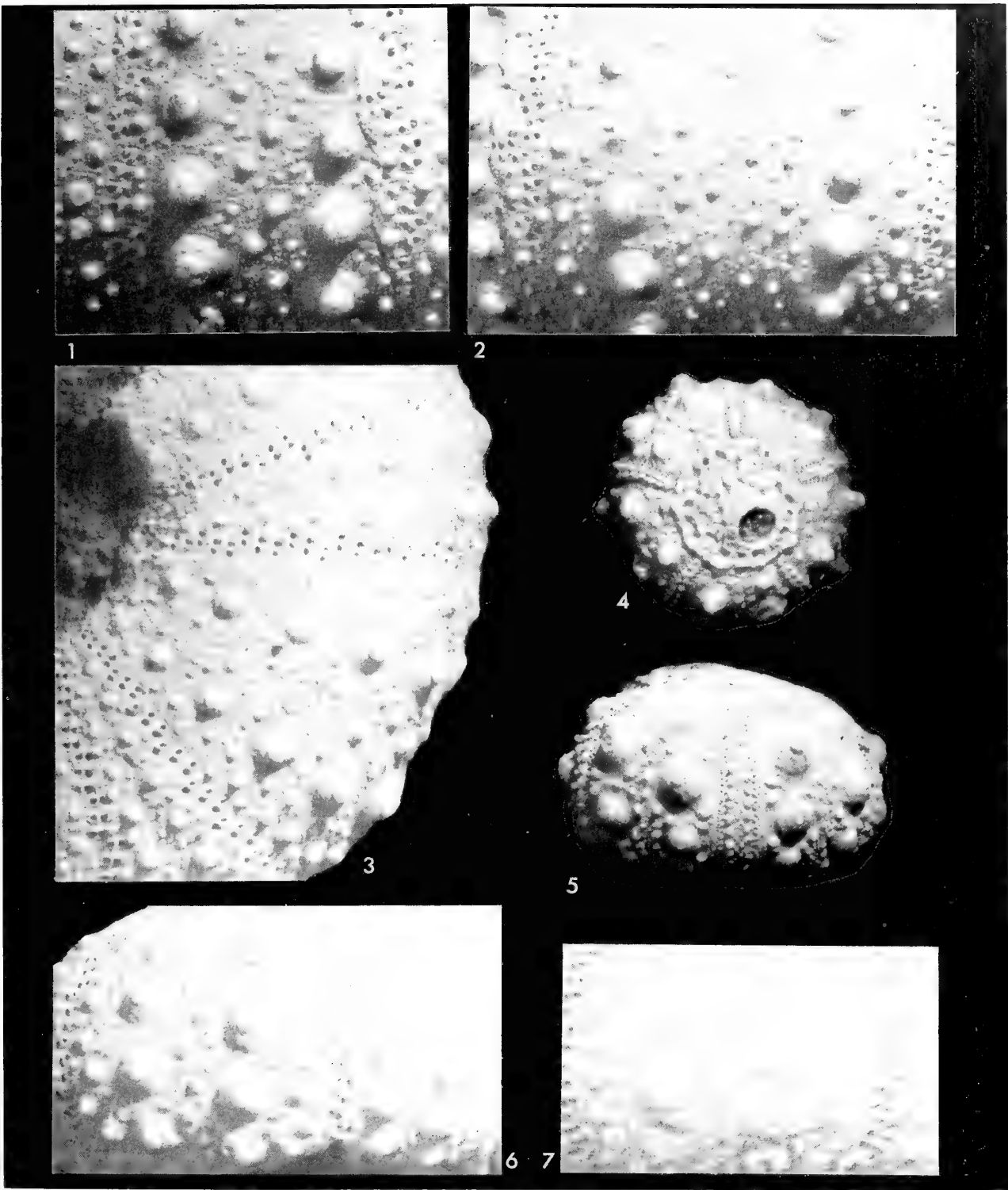
PLATE 17

Figs 1, 2 *Circopeltis? emiratus* sp. nov. BMNH EE3584, holotype, details of ambital tuberculation; **1**, ambulacrum, × 7; **2**, interambulacrum, × 5.

Figs 3, 6, 7 *Echinotiara perebaskinei* Lambert. **3, 6,** BMNH EE3774; **3**, apical, × 6; **6**, ambital detail, × 5. Jebel Rawdah, section 2, bed 4. **7,** BMNH EE3785, lateral detail, × 6. Jebel Rawdah, section 2, beds 6–8.

Figs 4, 5 *Salenia nutrix* Peron & Gauthier. **4,** BMNH EE3627, apical, × 5. Jebel Rawdah, section 1, bed 3. **5,** BMNH EE3634, lateral, × 5. Jebel Rawdah, section 2, loose in scree at level of bed 11.
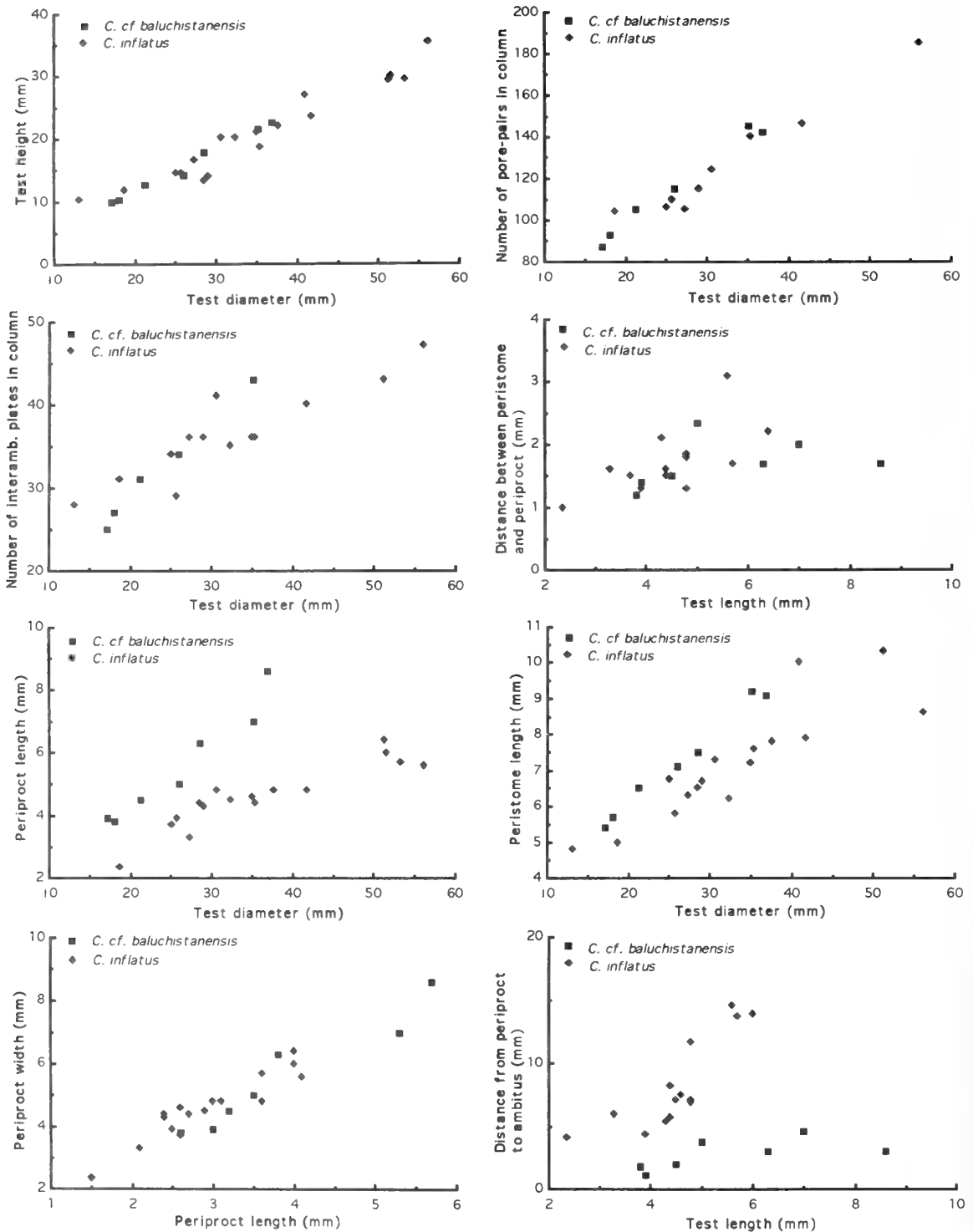
Fig. 42   Biometric data for *Coenholectypus inflatus* (Cotteau & Gauthier) and *C.* cf. *baluchistanensis* (Noetling).

4·6%, N = 16), being relatively larger in small individuals.

REMARKS. This species is easily recognised by its rounded profile, and its small periproct that lies close to the peristome and well separated from the ambitus. Although Cotteau & Gauthier's (1895) description is sketchy, it is readily recognis-

able from the illustrations given. Ali (1989) described two species of *Coenholectypus* from the western Oman mountains *C. inflatus* and *C. larteti* (Cotteau). Unfortunately the latter is a Cenomanian species (Smith *et al.* 1990). Because Ali gave no description and only illustrated the aboral surfaces of his

PLATE 18

Figs 1–6 *Coenholectypus* cf. *baluchistanensis* (Noetling). **1–3**, BMNH EE3389; **1**, apical; **2**, oral; **3**, lateral; all × 2. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation. **4–6**, BMNH EE 3395; **4**, apical; **5**, oral; **6**, lateral; all × 2. Jebel Rawdah, section 2, bed 11.

Figs 7–11 *Coenholectypus inflatus* Cotteau & Gauthier. **7**, BMNH EE4330; oral, × 1. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation. **8, 9**, BMNH EE3412; **8**, lateral; **9**, oral; both × 2. Jebel Buhays, section 2, lowest part of the Simsima Formation. **10, 11**, BMNH EE3424; **10**, apical; **11**, lateral; both × 1·5. Jebel Rawdah, section 3b, loose, from higher part of the section.

two forms, it is impossible to tell to which species either belongs. His assignment of one to *C. inflatus* is therefore accepted tentatively.

C. inflatus differs from *C.* cf. *baluchistanensis* (Noetling), the other species described here, on several counts. Firstly, it has finer tuberculation on its oral surface at comparable sizes. Secondly, its peristome is proportionally smaller at comparable sizes, and thirdly, its periproct is smaller and more removed from the ambitus at all sizes (Fig. 42).

There is a stratigraphical variation in profile. The taller forms, exactly comparable in form with the Iranian type, are found lower down in the sections in the coarse calcarenites: in bed 2 at Jebel Rawdah section 4, In bed 6 at section 2, and in bed 13 at section 4. The more depressed forms are found higher up in the more orbitoline-rich limestones and may represent deeper water morphological varieties.

Coenholectypus cf. *baluchistanensis* (Noetling, 1897)
Pl. 18, figs 1–6; Figs 42, 43B, D

cf. 1897   *Holectypus baluchistanensis* Noetling: 18, pl. 3, fig. 3.

MATERIAL. Thirteen specimens (BMNH EE3386–98).

OCCURRENCE. In the western Oman mountains this species was found at the following localities and horizons:
Jebel Buhays, section 1: loose in scree (3) and bed 8 (1).
Jebel Thanais, lowest 2 m of limestone section (1).
Jebel Rawdah, section 1: 20 cm below the top of bed 5 (1).
Jebel Rawdah, section 2: bed 11 (9).

It was originally described from the Maastrichtian of Baluchistan.

DESCRIPTION. Tests are circular in outline and range from 18–37 mm in diameter. They are moderately inflated in profile (Pl. 18, fig. 3), with a test height 55–62% of test length. The ambitus is rounded and lies a little below mid-height.

The apical disc has five gonopores. The four genital plates are small and pentagonal and separated from each other by ocular plates that are similar in size (Fig. 43D). The madreporite plate is large and often tumid. Madrepores are well developed over the central area.

Ambulacra are uniserial throughout, with simple nonconjugate pores. There is no hint of incipient biseriality adapically, nor any pore crowding adorally. All plates are simple, with triad development only appearing towards the peristome.

The interambulacra are standard in structure. The periproct is relatively large and opens between interambulacral plates 2a,b and 7a,b. It is oval in outline, pointed at both ends. Its width is 60–76% of its length (mean = 70%, SD = 5·7%, N = 7). It opens close to the peristome (Pl. 18, fig. 2; Fig. 43B), separated by 20–45% of the periproct length from the peristome (mean = 32%, SD = 8·4%, N = 7). It is separated from the ambitus by only a small distance in smaller individuals, some 28% of periproct length at 17 mm test length, but this increases in larger individuals to reach 65% of periproct length at a test length of 35–37 mm.

The peristome is circular in outline with deep and well marked buccal notches. It is 10–22·5% of test length in
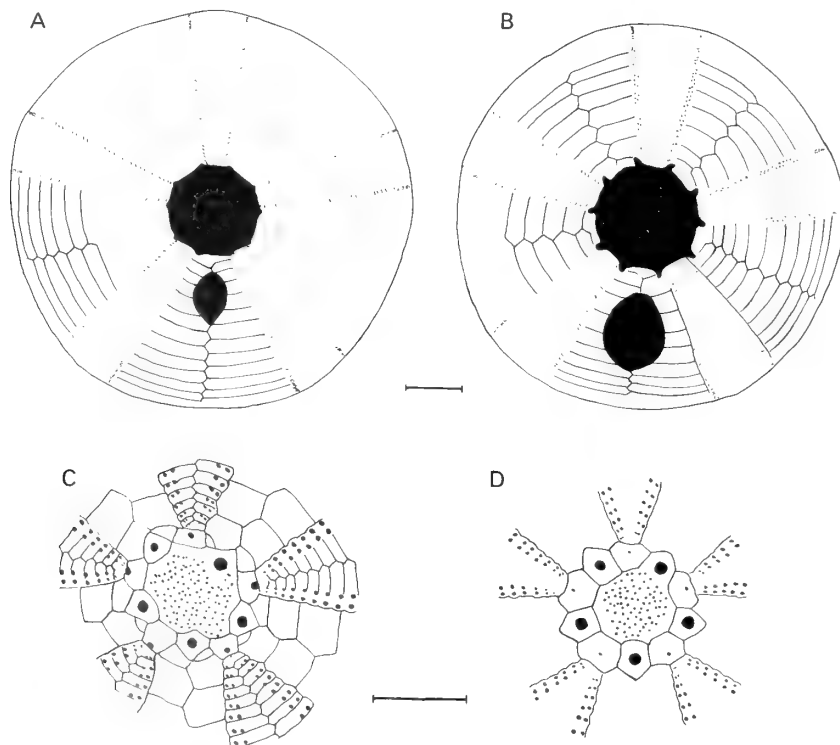
Fig. 43 Camera lucida drawings of plating in *Coenholectypus*. **A, C**, *C. inflatus* (Cotteau & Gauthier), BMNH EE3412: A, oral plating; C, apical disc. **B, D**, *C.* cf. *baluchistanensis* (Noetling), BMNH EE3389: B, oral plating; D, apical disc. Scale bars: A, B = 5 mm; C, D = 1 mm.

diameter (being relatively larger in small individuals).

REMARKS. This species is easily distinguished from the other *Coenholectypus* that occurs here, *C. inflatus*, by its larger peristome, larger periproct that extends much closer to the ambitus, and by its coarser adoral tuberculation. It also has deeper buccal notches.

C. baluchistanensis Noetling, from the Maastrichtian of Baluchistan, was established on the basis of two specimens 31 and 38 mm in diameter. Like the species described here, this has a relatively large peristome occupying much of the lower surface. Unlike the arabian specimens, the periproct of the Baluchistan species extends closer to the ambitus in the illustrated specimen. However, Noetling states that all specimens are crushed to some degree, and the illustrated specimen is damaged posteriorly. Therefore I suspect that the periproct is in reality slightly more distant from the ambitus than is actually shown. Until new material of *C. baluchistanensis* is available, the identification of Omani material as this species must remain tentative.

C. subcrassus Peron & Gauthier, from the early Maastrichtian of Algeria and Tunisia, differs from *C. baluchistanensis* in having a much larger periproct that occupies virtually the entire oral surface of the posterior interambulacrum. It is illustrated as having a broad, flat, adambital margin, unlike the arabian species. However, *C. subcrassus* and *C. baluchistanensis* are sister taxa.

Genus *COPTODISCUS* Cotteau & Gauthier, 1895

Coptodiscus magniproctus sp. nov. Pl. 19, figs 4–7; Figs 44, 45

TYPES. Holotype, BMNH EE3716, paratype, BMNH EE3715. There are no other specimens.

OCCURRENCE. Both specimens come from the base of the silty *Loftusia* beds (bed 1), at Jebel Huwayyah, section 2.

DIAGNOSIS. A *Coptodiscus* with a relatively large periproct occupying most of the oral surface of the posterior interambulacrum and opening between interambulacral plates 2 and 7. Aboral interambulacral ornament comprising a series of fine sutural pits and a set of pits along the midline of the each plate.

DESCRIPTION. Both specimens are small, but have open gonopores and are thus mature individuals. The smaller specimen is 10 mm in diameter, the larger 16 mm. Both are circular and low conical in profile, with the ambitus positioned relatively low down. Test height is about 40% of test diameter.

The apical disc is small and compact (Fig. 45A). There are five genital plates, each perforated by a gonopore. The ocular plates are almost as large as the genital plates, but are exsert and only oculars III and II abut the madreporite plate. The genital plates are contiguous around the posterior and lateral margins of the madreporite.

Ambulacra are uniserial and simple throughout, pores becoming slightly more widely spaced towards the peristome. There are three and a half ambulacral plates to an ambital interambulacral plate.

The peristome is relatively large, 25% of test diameter in diameter. It is not much invaginated. The periproct is relatively large, being 3·6 mm in length (22% of test diameter) by
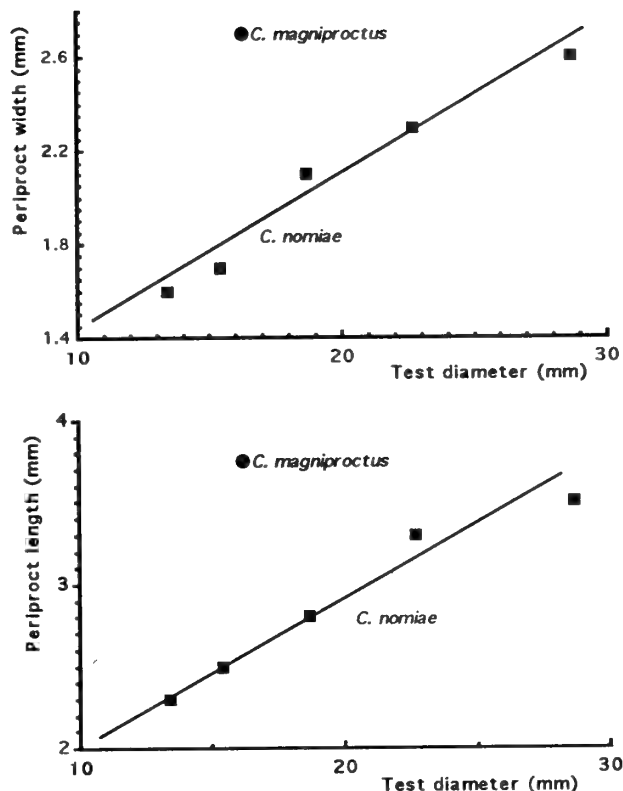
Fig. 44 Biometric data for species of *Coptodiscus*. Data from the type series of *Coptodiscus noemiae* Cotteau & Gauthier. The holotype of *C. magniproctus* sp. nov. is also plotted.
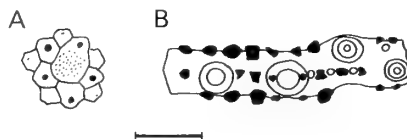
Fig. 45 Camera lucida drawings of *Coptodiscus magniproctus* sp. nov., BMNH EE3716. **A**, Apical disc; **B**, ambital interambulacral plate, adradial margin to right. Scale bar = 1 mm.

2·3 mm. It is pointed at both ends and lies close to both the peristome and the ambitus. Only 1·3 mm separates the periproct from the peristome and 1·2 mm separates the periproct from the ambitus. The periproct opens at interambulacral plate 2 and extends to interambulacral plate 7 (Fig. 44).

Tuberculation is standard with three or four primary tubercles on an ambital interambulacral plate. The surface of the test is ornamented by rows of fine pits (Pl. 19, fig. 4; Fig. 45B). These are arranged along the horizontal sutures, but are also developed along the midline of the plate in between the primary tubercles.

REMARKS. Amongst holectypoids, ornamentation of the test, as seen in this species, is found only in the genus *Coptodiscus*. Only one late Cretaceous species of *Coptodiscus* has ever been described, *C. nomiae* Cotteau & Gauthier (1895) (Pl. 19, figs 1–3; see Kier 1972 for a detailed description). *C. nomiae*, which comes from the 'Senonian' of south-
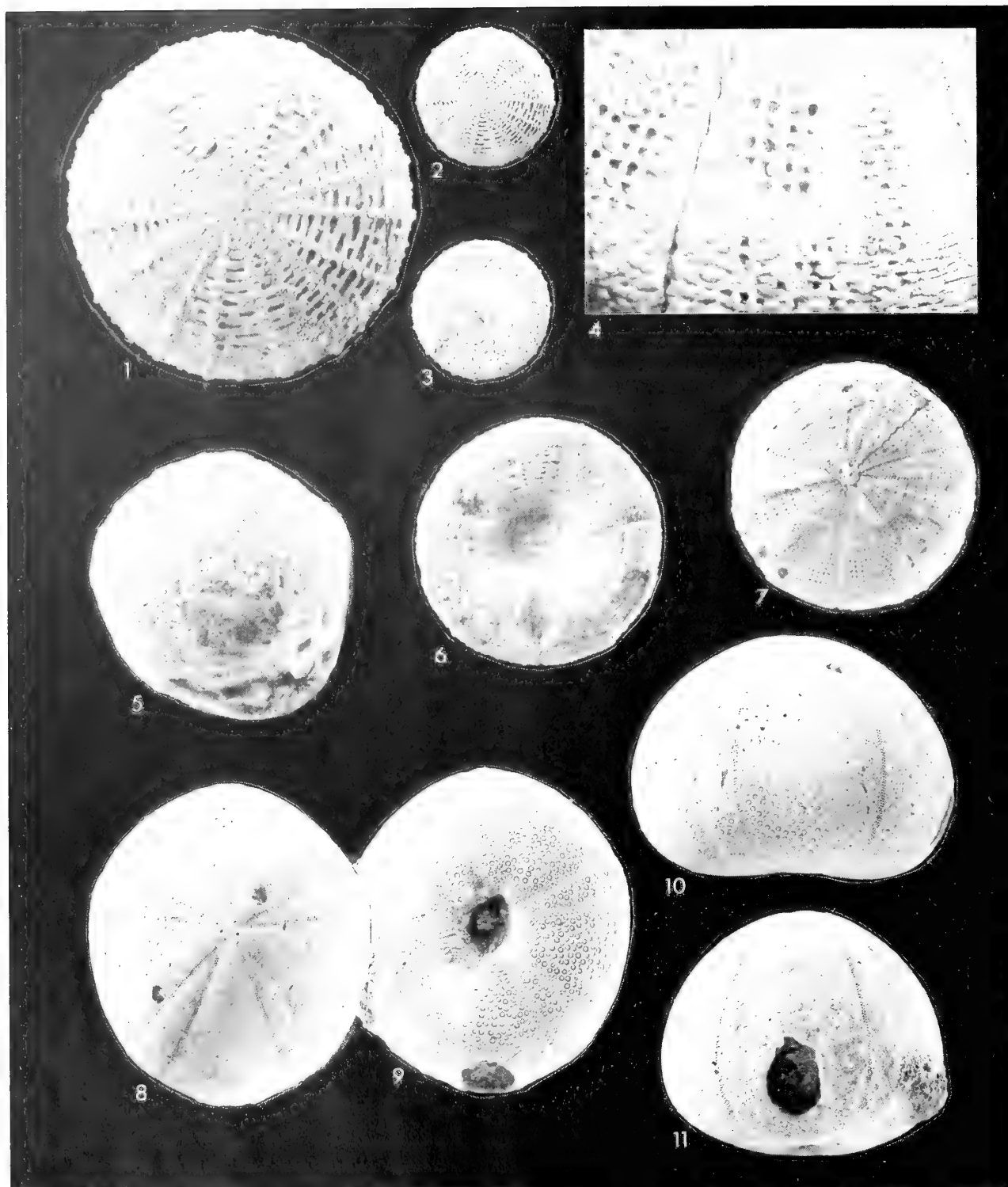
Figs 1–3   *Coptodiscus noemiae* Cotteau & Gauthier. Syntype, from the Morgan Collection, Museum d'Histoire Naturelle, Paris; **1**, apical, ×
   5; **2**, apical, × 2; **3**, oral, × 2; Senonian, Khianan, Iran.
Figs 4–7   *Coptodiscus magniproctus* sp. nov. Jebel Huwayyah, section 2, bed 1. **4, 6, 7**, BMNH EE3716, holotype; **4**, detail of adapical
   ornamentation, × 10; **6**, oral, × 3; **7**, apical, × 3. **5**, BMNH EE3715, paratype, apical surface, × 5.
Figs 8–11   *Conulus douvillei* Cotteau & Gauthier. BMNH EE4306; **8**, apical; **9**, oral; **10**, lateral; **11**, posterior; all × 2. Jebel Thanais, lowest
   2 m of the Simsima Formation.
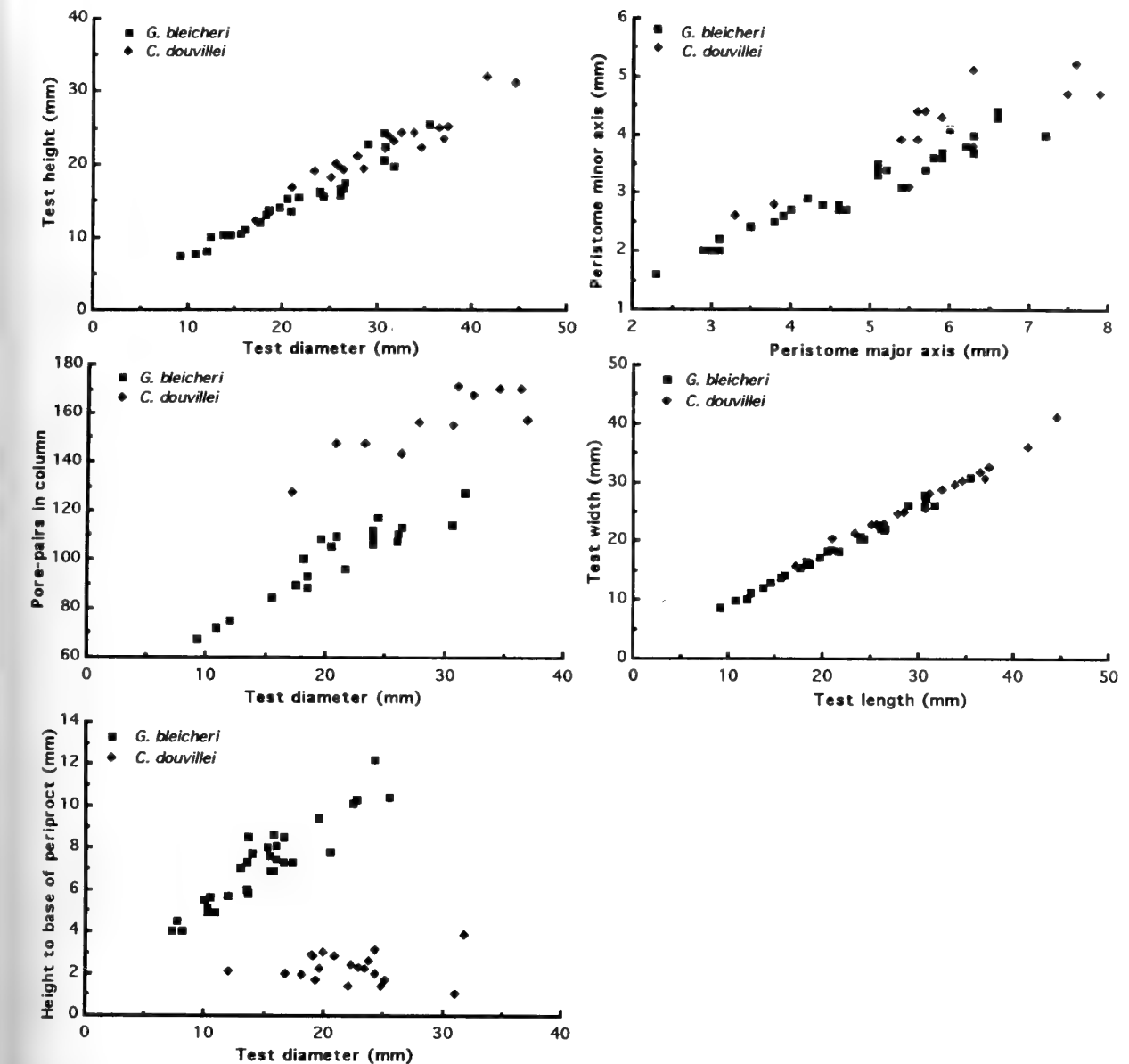
Fig. 46 Biometric data for '*Globator*' *bleicheri* (Thomas & Gauthier) and *Conulus douvillei* (Cotteau & Gauthier).

ern Iran and the late Campanian of Saudi Arabia and Oman, differs from our species in several important details. Firstly, its periproct is very much smaller at comparable sizes (Fig. 44) and it lies well separated from the peristome, with at least three and usually four interambulacral plates in each column separating the two openings, as opposed to the two in *C. magniproctus*. The periproct is also considerably more rounded in *C. nomiae*. A second immediately apparent difference is in the style of ornamentation developed aborally. In *C. nomiae* there is a single laterally extensive sutural pit on either side of the primary tubercle, also, intraplate pits are not as well developed, whereas in *C. magniprocta* there is a well-developed row of sutural pits (compare Pl. 19, figs 1, 4).

Family **CONULIDAE** Lambert, 1911
Genus '*GLOBATOR*' Agassiz, 1840

REMARKS. The genus *Globator* was erected by Agassiz (1840) for small, ovoid conulids with large periprocts opening above the ambitus. The type species is *Globator nucleus* Agassiz, but this is based on a juvenile *Conulus rotundus* Goldfuss and thus *Globator* falls into synonymy with *Conulus*. However, there is a distinct clade of ovoid conulids with large, supra-ambital periprocts that can be recognized. This group is currently under revision (Smith & Wright, in prep.) and for the moment we retain its members under the name '*Globator*'.

'Globator' bleicheri (Gauthier, 1889)   Pl. 20, figs 1–10;
Figs 46, 47A, B, F–I, 48A

1889   *Pyrina bleicheri* Gauthier: 51, pl. 3, figs 15–18.
1895   *Pyrina orientalis* Cotteau & Gauthier: 68, pl. 11, figs
        1–8.
1897   *Pyrina zumoffeni* de Loriol: 158, pl. 7, fig. 1.
1967   *Pyrina ovulum* Agassiz; Devries: 177, pl. 5, figs 19–21.
1987   *Pseudopyrina bleicheri* (Thomas & Gauthier);
        Zhagbib-Turki: 167.
1989   *Globator orientalis* (Cotteau & Gauthier); Ali: 403,
        fig. 5 (4–5).

MATERIAL STUDIED. This is a common species in the lower
beds of the Simsima Formation and a large number of
specimens were available for study. There are 208 specimens
in the collections made. Of these the following were mea-
sured: BMNH EE4107, EE4116–19, EE4121, EE4129,
EE4130, EE4132–34, EE4139–41, EE4144–45, EE4154–57,
EE4163, EE4172, EE4174, EE4186, EE4208, EE4217,
EE4232, EE4249, EE4251, EE4253–54, EE4257.

OCCURRENCE. The species was first described from the late
Cretaceous (late Campanian) of Jebel Atra, Tunisia. It has
also been described from the Upper Senonian of Derre-i-
Chahr and Endjir-kouh, southern Iran (Cotteau & Gauthier
1895) and the late Cretaceous of Palestine (de Loriol 1897)
and Turkey (Devries 1967). In the western margins of the
central Oman Mountains this species is found at the following
localities and levels:
Jebel Buhays, section 1: loose in scree (96).
Jebel Buhays, section 2: loose in scree (3).
Jebel Buhays, section 3: lowest 2 metres (1).
Jebel Thanais: lowest couple of metres of section (5).
Jebel Aqabah: basal shell bed (2).
Jebel Faiyah, section 1: arbaciid level *ca.* 4 m above base
(12).
Jebel Huwayyah, section 1: beds 14 and 15 (54).

Jebel Rawdah, section 1: bed 6 (1); top of bed 4 (15); bed 3
(49); loose (2).
Jebel Rawdah, section 2: bed 6 (1); bed 11 (10); bed 13 (1);
bed 14 (7); bed 16 (3); bed 19 (8); bed 20 (1); bed 21 (1)
loose in scree just above bed 12 (2); loose in scree, mostly
near base (14).
Jebel Rawdah, section 3: bed 1 (11); bed 5 (9); bed 9 (1); bed
11 (1); loose in scree (3).
Jebel Rawdah, section 4: bed 2 (9); bed 4 (4); bed 5 (1); bed 8
(3); bed 10 (10); bed 14 (3); bed 20 (1).

DIAGNOSIS. An oval, rather depressed *'Globator'* with a
large, strongly ellipsoidal peristome. The periproct lies high
on the posterior surface and is visible from above but not
from below. Pore-pairs in weak arcs only towards the peris-
tome, not forming multiple rows. Genital plates 3 and 4
separated by ocular plate IV in adults.

DESCRIPTION. Tests range from 9 to 35 mm in length and are
oval in outline and profile. Test width is 82–91% of test
length (mean = 86%, SD = 2·6%, N = 32; Fig. 46) with the
widest point on the test coincidental with the posterior
portion of the anterior ambulacra. Test height is 61–80% of
test length (mean = 70%, SD = 5·3%, N = 32) and the tallest
point on the test is subcentral. Tests in profile have a
relatively broad, flat apex and base and a rounded ambitus
(Pl. 20, figs 3, 8).
  The apical disc is more or less central and is tetrabasal (Fig.
47F–H). Genital plate 2 is considerably larger than the other
four genital plates and is covered in madrepores. Genital
plate 3 is the smallest and in the great majority of specimens
is separated from genital plate 4 by ocular plate 4, which
abuts genital plate 2. Genital plates 3 and 4 are found in
contact only in small individuals. The posterior pair of genital
plates are in contact posterior to genital plate 2. Ocular plates
are pentagonal in outline and project.
  Ambulacra are uniserial and pore-pairs are undifferenti-
ated. Above the ambitus they are very strictly uniserial (Fig.
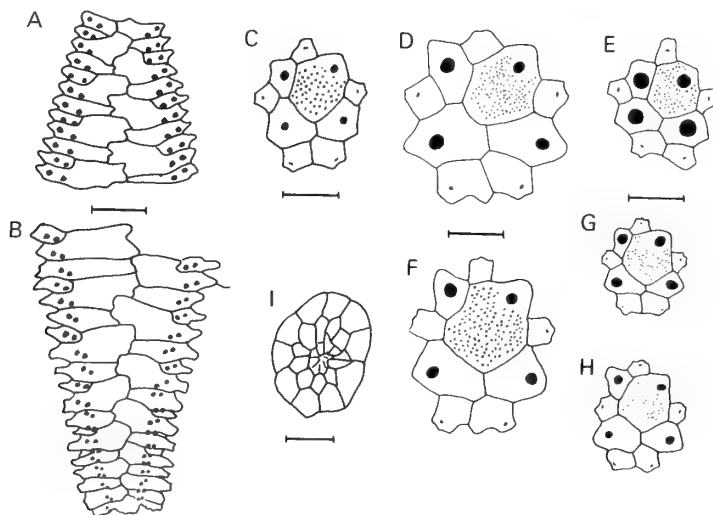
Fig. 47   Camera lucida drawings of plating in *'Globator'* and *Conulus*. **A, B, F-I**, *'G.' bleicheri* (Thomas & Gauthier). A, B, BMNH EE4187;
A, adapical ambulacral plating; B, adoral ambulacral plating, peristomial margin at base; F, BMNH EE4186, apical disc; G, BMNH
EE4148, apical disc; H, BMNH EE4154, apical disc; I BMNH EE4151, peristomial plating. **C-E**, *Conulus douvillei* (Cotteau & Gauthier),
apical disc plating: C, BMNH EE4204; D, BMNH EE4277; E, BMNH EE4211. Scale bars = 1 mm.
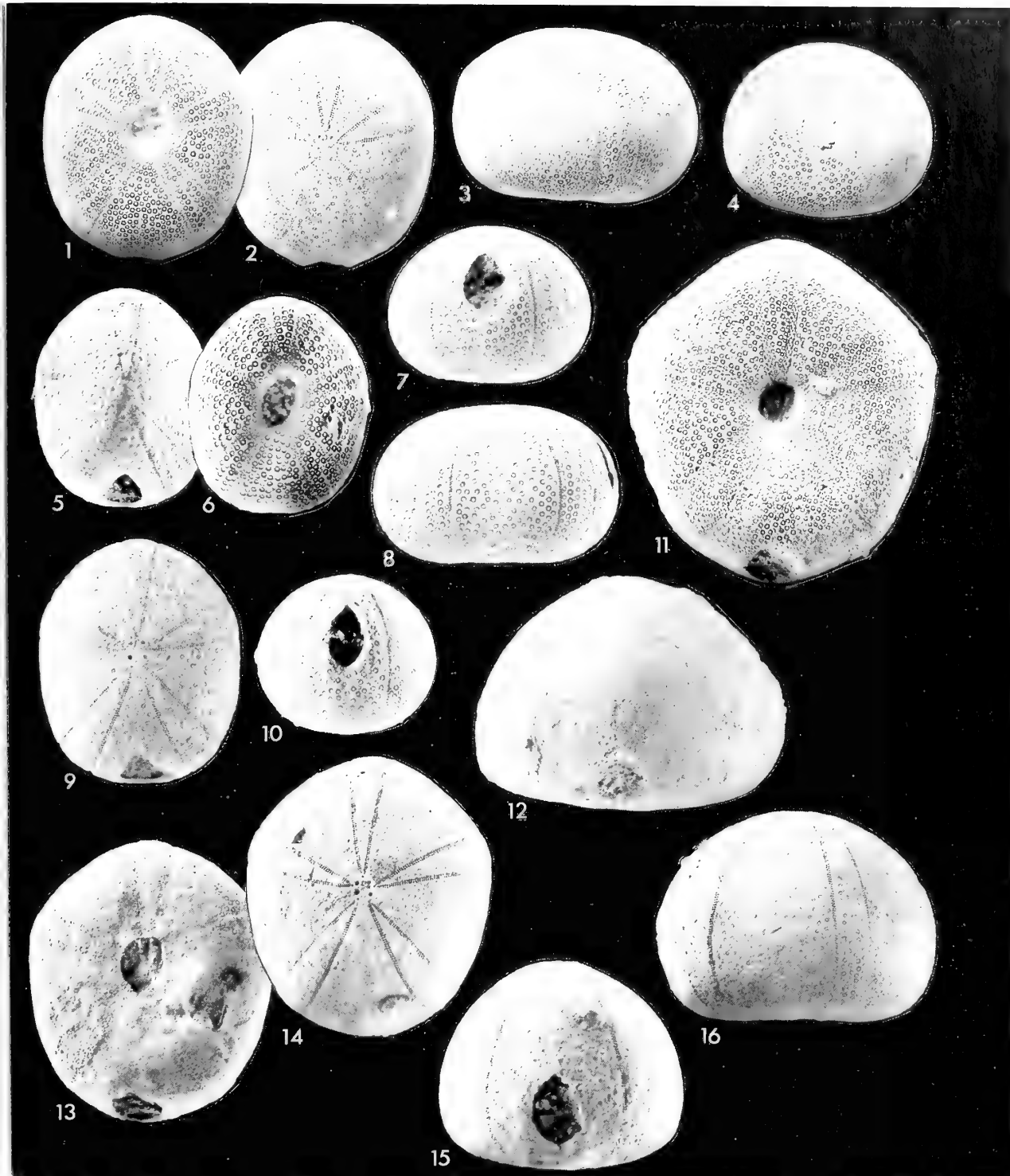
LATE 20

igs 1–10 '*Globator' bleicheri* (Peron & Gauthier). **1–4,** Topotype specimen of *Pyrina orientalis* Cotteau & Gauthier, from the Morgan
  Collection, Museum d'Histoire Naturelle, Paris; **1**, oral; **2**, apical; **3**, lateral; **4**, posterior; all × 2. Senonian, Poucht-e-Kouk, Iran. **5, 6, 10,**
  BMNH EE4251; **5**, apical; **6**, oral; **10**, posterior; all × 2. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the
  Simsima Formation. **7–9,** BMNH EE4208; **7**, posterior; **8**, lateral; **9**, apical; all × 2. Jebel Buhays, section 1; loose in the scree derived from
  the lowest 3 m of the Simsima Formation.
igs 11–16 *Conulus douvillei* (Cotteau & Gauthier). **11, 12,** topotype specimen from the Morgan collection, Museum d'Histoire Naturelle,
  Paris; **11**, oral; **12**, lateral; both × 2. Senonian, Khianan, Iran. **13–16,** BMNH EE4308; **13**, oral; **14**, apical; **15**, posterior; **16**, lateral; all ×
  2. Jebel Thanais, lowest 2 m of the Simsima Formation.
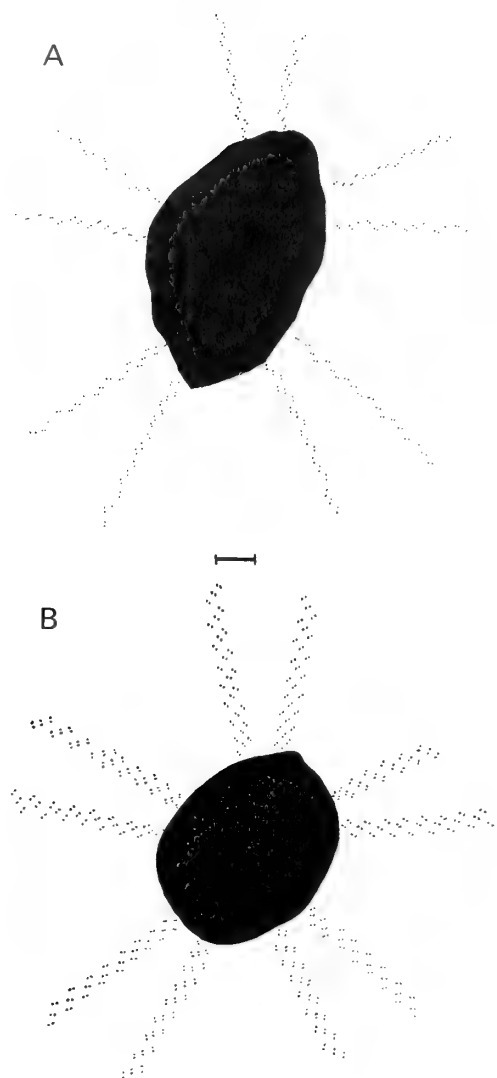
Fig. 48 Camera lucida drawings of adoral pore arrangement. **A**, '*Globator' bleicheri* (Thomas & Gauthier), BMNH EE4187; **B**, *Conulus douvillei* (Cotteau & Gauthier), BMNH EE4309. Scale bar = 1 mm.

47A), but towards the peristome they become weakly arcuate and reduce in pore-diameter size (Figs 47B, 48A). There are about 88 pore-pairs in a column at 18 mm test length, rising to 127 at 32 mm test length (Fig. 46). Plates are compound in the pyrinoid style, with a single small demiplate in each triad (Figs 47A, B). All plate sutures are denticulate.

The periproct is large and tear-drop shaped, pointed adapically (Pl. 20, figs 7, 10). It lies on the posterior surface relatively high on the test, so that it is visible when viewed from above, but not from below. Periproct height is 28–46% of the test height (mean = 36%, SD = 4·6%, N = 29) and periproct width is 56–80% of its height (mean = 65%, SD = 5·8%, N = 27). The distance from the base of the periproct to the base of the test is 38–62% of the test height (mean = 49%, SD = 5·6%, N = 31).

The peristome is oblique and broadly fusiform in outline, with the long axis running from interambulacrum 3 to ambulacrum I (Pl. 20, fig. 6). There is hardly any invaginated lip

developed around the peristome, although the oral surface does curve inwards towards the periproct slightly.

Tuberculation is uniform throughout, with semi-regular and slightly sunken primary tubercles scattered over the surface, surrounded by a very dense miliary granulation. There is no internal butressing.

REMARKS. This species is easily distinguished from the other species of Conulidae, *Conulus douvillei*, that occurs here. *C. douvillei* has a periproctal opening that lies close to the base of the test, whereas the periproct in '*G.' bleicheri* lies high on the posterior and is separated by a considerable distance from the base. This is not a size-related character since there is clear separation of the two species at all sizes (Fig. 46). A second difference concerns the development of phyllodes adorally. In '*G.' bleicheri* the pore-pairs become slightly arcuate adorally (Fig. 48A), but even in the largest specimens they never become triserially arranged. Adoral pore-pairs in *C. douvillei*, by contrast, are arranged triserially across much of the oral surface (Fig. 48B). Finally, in the apical disc plating of '*G.' bleicheri* genital plate 2 almost always reaches to ocular IV separating genital plates 3 and 4. In *C. douvillei* genital plate 2 does not reach ocular plate IV and genital plates 3 and 4 maintain firm contact.

This species has previously been recorded from the Oman mountain region by Ali (1989) and Smith (in Skelton *et al.* 1990) under the name *Globator orientalis* (Cotteau & Gauthier). '*G.' orientalis* (Pl. 20, figs 1–4) was described from the late Cretaceous of southern Iran by Cotteau & Gauthier (1895). However, it appears virtually indistinguishable in form to '*Globator' bleicheri* Thomas & Gauthier, from the late Campanian of Tunisia (Zhagbib-Turki 1987). The only slight difference between these two forms is that '*G.' orientalis* may have a slightly smaller peristome. For the present, however, the two species are synonymized.

Genus *CONULUS* Leske, 1778

Conulus douvillei (Cotteau & Gauthier, 1895)   Pl. 19, figs 8–11; Pl. 20, figs 11–16; Figs 46, 47C–E, 48B

1895   *Echinoconus douvillei* Cotteau & Gauthier: 70, pl. 11, figs 9–13.
1932   *Pyrina mortenseni* Checchia-Rispoli: 21, pl. 2, figs 1–3, pl. 3, figs 1, 2.
?1967   *Conulus douvillei* (Cotteau & Gauthier); Devries: 184, pl. 5, figs 22–25.
1972   *Globator mortenseni* (Checchia-Rispoli); Kier: 70, figs 35, 36, pl. 44, figs 1–7.
1989   *Globator mortenseni* (Checchia-Rispoli); Ali: 403, Fig. 4 (6–7).

TYPES. The syntypes are the five specimens whose dimensions are cited by Cotteau & Gauthier (1895: 70). They may be represented amongst material in either the Cotteau Collection (Lyon) or the Morgan Collection (Museum d'Histoire Naturelle, Paris), but none have been definitely identified.

MATERIAL STUDIED. This species is less common than '*Globator' bleicheri*, but is never the less well represented in the collections. There are 39 specimens, of which the following were measured: BMNH EE4211, EE4250, EE4277, EE4279–80, EE4283, EE4285, EE4287, EE4291, EE4898–99, EE4301, EE4304–06, EE4308, EE4310.

OCCURRENCE. This species is found in the western Oman Mountains at the following levels:

Jebel Huwayyah, section 1: beds 3–5 (1).

Jebel Buhays, section 1: loose, derived from lowest few metres of section (19).

Jebel Thanais: lowest few metres of the Simsima Formation (11).

Jebel Rawdah, section 2: bed 14 (1); bed 15 (2); bed 21 (3); loose, mid-section (1).

Jebel Rawdah, section 3: loose (4).

Jebel Rawdah, section 4: beds 8/9 (1); bed 13 (1); loose in scree (1).

Outside Oman, the species is known from Libya, Saudi Arabia, southern Iran and Assam, India.

DIAGNOSIS. A species of *Conulus* with a rounded to strongly fusiform peristome which is not sunken. Periproct situated relatively low on the posterior surface, not visible from above. Pore-pairs adorally arranged triserially. Apical disc with genital plates 3 and 4 always in contact. Test profile subconical.

DESCRIPTION. Tests range from 17 to 45 mm in length and are ovoid to rounded pentagonal in outline. Test width is 82–96% of test length (mean = 88%, SD = 3·2%, N = 18) and the widest point coincides with the posterior part of the antero-lateral ambulacra. Test height is 64–81% of test length (mean = 72%, SD = 4·9%, N = 20) and in profile the test has a broad, flat base and is rounded subconical above (Pl. 20, figs 11–16).

The apical disc lies centrally and is tetrabasal. Genital plate 2 abuts the other three genital plates but never reaches ocular plate 4 to separate genital plates 3 and 4 (Figs 47C–E). Genital plates 4 and 1 are always in contact behind the madreporite. There appears to be some degree of differentiation in gonopore size, suggestive of sexual dimorphism.

Ambulacra are straight and compound in the pyrinoid style. Above the ambitus pore-pairs are strictly uniserial, but below the ambitus they become offset into three discrete columns and these continue to the peristome edge (Pl. 19, fig. 9; Pl. 20, fig. 11; Fig. 48B).

The periproct lies on the posterior border, close to the base (Pl. 20, fig. 15). It is tear-drop shaped, being pointed adapically. Its height is 28–40% of the test height (mean = 35%, SD = 3·2%, N = 20) and its width is 55–77% of its height (mean = 65%, SD = 6·2%, N = 19). The base of the periproct lies 3–17% of the test height above the base (mean = 11%, SD = 3·6%, N = 20). The periproct is just visible from beneath, but is not seen from above (Pl. 19, figs 8, 9).

The peristome is oval to fusiform in outline and is not invaginated, although the oral surface may be slightly depressed towards the peristome. Its length is 14–23% of the test length (mean = 20%, SD = 2·7%, N = 13). Its width is 56–81% of its length (mean = 70%, SD = 8·1%, N = 13). It is oblique, with its long axis orientated from interambulacrum 3 to ambulacrum I (Pl. 19, fig. 9).

REMARKS. The distinction between this species and '*Globator*' *bleicheri* is detailed above. This species comes closest to *Conulus giganteus* Noetling (*C. gigas* Cotteau, *C. ataxaensis* Cotteau) but in this species complex the peristome is less ovoid and is distinctly more invaginated than *C. gigas* at least. Whether the Middle Eastern species turn out to be sufficiently distinct remains to be seen.

Order **CASSIDULOIDA** Claus, 1880
Family **CLYPEOLAMPADIDAE** Kier, 1962

DIAGNOSIS (following Kier, 1962). Cassiduloids with a domed test and flat base. Petals long and straight, apical disc tetrabasal, periproct inframarginal and transverse, bourrelets with three or more columns of pores and with buccal pores present.

TYPE GENUS. *Clypeolampas*, type species *C. ovatus* Lamarck, 1816.

OTHER GENERA INCLUDED. *Hungaresia* Szorenyi, type species *Hungaresia hungarica* Szorenyi (junior synonym of *Clypeolampas ovum* Grateloup); *Vologesia* Cotteau & Gauthier, type species *V. tataosi* Cotteau & Gauthier.

REMARKS. Lambert (1919) claimed that the original figure and description of *Clypeolampas ovatus* Lamarck (1816: 22) was inadequate for certain identification, and thus used the name *Clypeolampas leskei* Goldfuss (1829) as the oldest available name. However, Kier (1962: 190) accepted *C. ovatus* Lamarck as a valid designation and sunk *C. leskei* Goldfuss in synonymy.

There are eighteen nominal species assigned to the three genera listed above. The differentiation of the three genera is, however, unclear. *Vologesia* was established by Cotteau & Gauthier (1895: 65) for a late Cretaceous species from Aftab, Iran, *V. tataosi* Cotteau & Gauthier. This is based on a single small individual, subcircular in plan view, with poorly developed bourrelets and the peristome positioned close to the anterior border. No other species were included in this genus until Lambert (1919) revised the then known members of *Clypeolampas*. He separated species into two groups; those with uniform aboral tuberculation, all tubercles being scrobiculate, and those forms which had a second kind of aboral tuberculation composed of nonscrobiculate pustules. The former he assigned to *Vologesia*, the latter to *Clypeolampas*. Lambert (1919) placed the following species in *Vologesia*: *C. ovum* Grateloup, *C. acuta* Desmoulins, *C. conica* Arnaud, *C. toucasi* Lambert, *C. gossauviensis* Lambert and a small undescribed Maastrichtian form. In *Clypeolampas* Lambert placed *C. leskei* Goldfuss [=*C. ovatus* Lamarck], *C. perovalis*, Arnaud, *C. orbicularis* Arnaud, *C. lestelei* Cotteau, *C. vishnu*, Noetling, *C. douvillei* Lambert and *C. mengaudi* Lambert.

In 1955, Szorenyi erected the genus *Hungaresia* for the new Santonian species *H. hungarica* Szorenyi of Hungary. This species appears to be identical in many important respects to the common Santonian species *Clypeolampas ovum* Grateloup, and Kier (1962: 191) synonymized the two genera, making *Hungaresia* a junior synonym of *Vologesia*.

Kier (1962, 1966) followed Lambert's generic differentiation, distinguishing *Clypeolampas* from *Vologesia* by its nonscrobiculate pustules developed adapically, and by its better developed floscelle. However, Kier's concept of *Vologesia* was based not on the type species but on *Clypeolampas ovum* Grateloup and is thus misleading.

There are very few stable characters on which to subdivide the group, the following being amongst the most informative.

(1) Aboral pustules developed. In some species there are characteristic pustules over the adapical surface that are slightly larger than the normal tuberculation and give the surface a rugose appearance. These are not tubercles for spine articulation, as they have no articular surface or sur-

rounding scrobicule. Instead they resemble the pustular calcite formed in species of *Conulus* or *Echinoneus* (Smith 1980). Their function is unknown but it may be to do with deterring parasitic and commensal settlement. Pustules are developed in a number of species, including the type *C. ovatus* Lamarck.

(2) The position of the peristome seems highly stable and distinctive. In *Vologesia tataosi* and *V. rawdahensis* the peristome lies close to the anterior border, with the anterior edge lying between 20 and 25% of the test length from the anterior. In almost all other species the peristome is subcentral, lying between 30 and 40% of the test length from the anterior. Only one species, *Clypeolampas toucasi* Lambert is intermediate in this respect, with its peristome between 25 and 30% of test length from the anterior.

(3) Elongation of the peristome. Only *Vologesia rawdahensis* Ali has such a laterally elongate peristome. In other species the peristome is suboval.

(4) The degree to which the floscelle projects as prongs over the peristome is to some extent size dependent, with more prominent floscelles in larger individuals. However, at a similar size it is apparent that *Vologesia tataosi*, *V. rawdahensis* and *Clypeolampas toucasi* show virtually no floscelle development, whereas *C. ovatus* and its synonyms and *C. perovalis* have very pronounced floscelle projection. In *C. lestelei*, *C. ovum*, and *C. conicus* as well as probably *C. helios*, the floscelle is slightly swollen but not projecting.

(5) The periproct is usually unambiguously positioned on the flat oral surface, but in a few species such as *C. helios* and *C. ovum*, the periproct lies subambitally because of the strongly inflated test profile.

(6) The apical disc is definitely tetrabasal in *C. lestelei*, *C. ovum* and *Vologesia rawdahensis*, but monobasal in *C. ovatus*.

(7) The arrangement of pores in the bourrelets, though to some extent size dependent, offers some differentiation. In *C. ovatus* there are many pores irregularly scattered between inner and outer columns in each half ambulacrum. By contrast *C, ovum* and *Hungaresia hungarica* have only the inner and outer series of pores. If *C. conicus* is just a variety of *C. ovum* as is suspected, then some specimens may have a few pores forming a mid row. The same is true of *Vologesia rawdahensis* where individuals have either two or three rows.

From this the following supraspecific taxonomy is proposed:

Clypeolampas Lamarck: Large forms with moderate to well developed bourrelets, subcentral peristome and aboral calcite pustules. Species included; *C. ovatus* Lamarck (includes *C. leskei* Goldfuss, *C. mengaudi* Lambert, *C. douvillei* Lambert, *C. orbicularis* Arnaud), Upper Campanian-Maastrichtian of Spain, southern France, Turkey; *C. perovalis* Arnaud, Lower and Middle Campanian of Gironde, France; ?*C. lestelei* Cotteau, ?Danian of Saint Cirac, Ariège, France.

Vologesia Cotteau and Gauthier. Distinguished from *Clypeolampas* by its anterior peristome without floscelle development. Type species *V. tataosi* Cotteau & Gauthier, Upper Senonian of Louristan, Iran; *V. rawdahensis* Ali, Maastrichtian of the Oman Mountains; *V. toucasi* (Lambert), Campanian of the Pyrenees, France.

Hungaresia Szorenyi. Smaller, ovoid forms with subcentral, pentagonal peristome with swollen but not projecting floscelles, no aboral pustules and subambital rather than fully adoral periproct. Type species, *H. ovum* (Grateloup)

[includes *H. hungarica* Szorenyi], Upper Santonian of France, Pyrenees, Hungary. Other species included: *H. helios* (Noetling), ?Maastrichtian, Mari Hills, Baluchistan.

Unplaced taxa: *Clypeolampas conicus* Arnaud (U. Santonian to L. Campanian, SW France) and *C. acuta* Desmoulins (pores in bourrelets shown as forming two columns only). material of these species has not been seen and so they cannot be placed with any confidence from the published descriptions and figures.

C. vishnu Noetling: based on a single worn specimen, inadequately known *nomen dubium*.

C. gossaviensis Lambert: based on a single, poorly preserved specimen and indeterminate from description and figure *nomen dubium*.

Genus *VOLOGESIA* Cotteau & Gauthier, 1895

TYPE SPECIES. *Vologesia tataosi* Cotteau & Gauthier, 1895, by original designation.

OCCURRENCE. Late Cretaceous ('Upper Senonian') of Iran; Maastrichtian of the United Arab Emirates and Oman.

DIAGNOSIS. Clypeolampadids with an anteriorly positioned peristome lying 20–30% from the anterior border. Peristome wide, pentagonal with bourrelets hardly developed. Phyllodes with two or three rows of pores in each half ambulacrum. Apical disc tetrabasal.

REMARKS. *Vologesia* is distinguished from *Clypeolampas* by its lack of aboral pustules and its poorly developed floscelles and bourrelets. It is distinguished from *Hungaresia* by its lack of floscelles, its more transverse peristome and its more anterior peristome.

Vologesia rawdahensis Ali, 1989   Pl. 21, figs 1–5; Figs 49–51

1989   *Vologesia rawdahensis* Ali: 406, fig. 5 (13).

TYPES. Three specimens in the Geology Museum, United Arab Emirates University, Al Ain, United Arab Emirates.

MATERIAL STUDIED. Seven specimens, of which five (BMNH EE3383–85, EE4326, EE4329) are well enough preserved to be included in the biometric analysis.

OCCURRENCE. This species is known only from the Simsima Formation of the western margins of the Oman Mountains. Specimens were found at the following localities and horizons:

Jebel Buhays, section 1: loose in the scree, derived from the lowest few metres of Simsima Formation (5).

Jebel Buhays, section 2: loose in the scree, derived from the lowest 2 m of Simsima Formation (1).

Jebel Thanais: lowest 2 m of Simsima Formation (1).

Jebel Rawdah, section 2: bed 19 (1).

Jebel Rawdah, section 3: bed 8 (1).

DESCRIPTION. Tests are flat-based and rounded to subconical in profile (Pl. 21, figs 1–4), with a relatively sharp ambitus situated low down. In outline the test is ovoid with a rounded anterior and a distinctly more pointed posterior. Tests range in length from 46 to 68 mm. Test width is 75–77% of test length and test height 53–62% of test length (Fig. 49). The tallest part of the test is central or slightly anterior of centre.
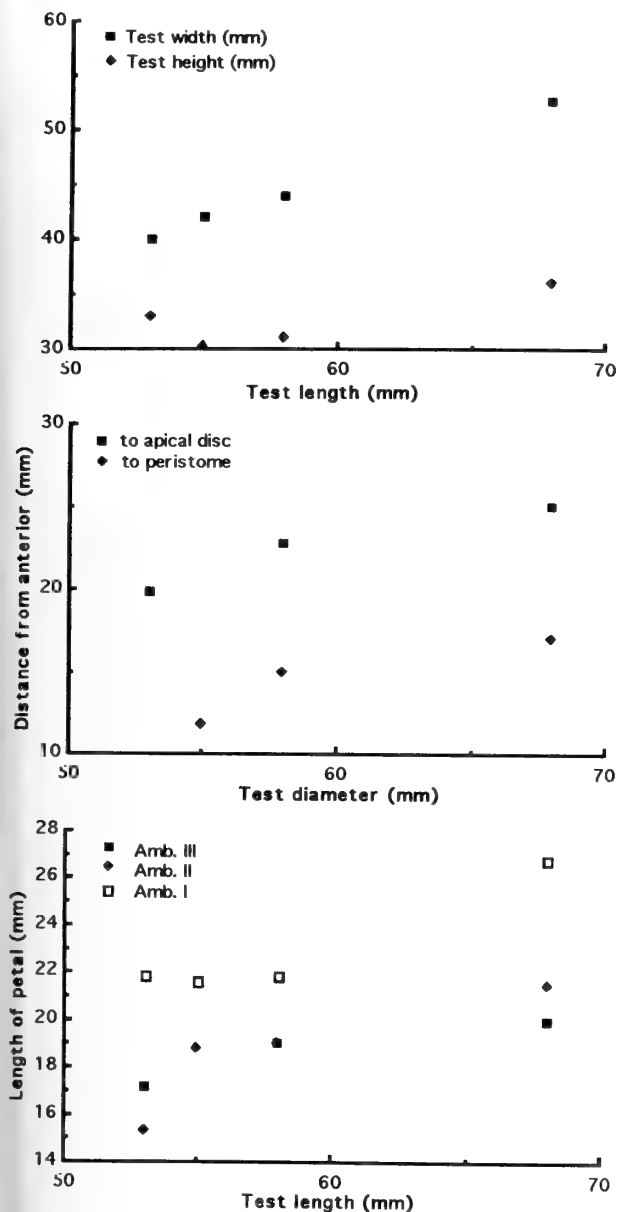
Fig. 49 Biometric data for *Vologesia rawdahensis* Ali.

The apical disc is tetrabasal (Fig. 51B), with the madreporite very large and occupying the centre. Other genital plates are much smaller and pushed far out into the adjacent interambulacra. The apical disc lies 37–39% of test length from the anterior border (Fig. 49).

Petals are relatively long and straight or only very slightly bowed. They are open distally and extend most of the distance towards the ambitus. The posterior petals are always slightly longer than the anterior three petals. They are composed of an inner circular pore and a highly elongate outer slit-like pore, joined by a furrow. There are 51 pores in a petal column in a 53 mm individual and 57 in a 68 mm individual. Pores below the petal are all single.

The peristome is pentagonal in outline and very much wider than long (width is 1·7–2·0 times greater than length).

It is straight sided and only slightly invaginated (Pl. 21, fig. 5; Fig. 50) and bourrelets are hardly developed. It lies 21–27% of the test length from the anterior border. Phyllodes are relatively short and are not depressed in the slightest. In some individuals there are only two columns of pores in each half ambulacrum, whereas in others there are three columns. The outer series is composed of about 12 pores, the inner series of 7 or 8 pores and the mid series, where present, of 4 or 5 pores (Fig. 51). The inner and middle series of pores are borne on occluded plates. Buccal pores are present.

The periproct lies on the oral surface at the posterior. It is oval in outline, approximately twice as wide as long and approximately the same size as the peristome.

Aboral tuberculation is fine and uniform, oral tuberculation slightly coarser and becoming less dense towards the midline. There is a broad tubercle-free band down the midline in the posterior interambulacrum running between the peristome and periproct. This is lightly pitted (Pl. 21, fig. 5).

REMARKS. This species was erected by Ali (1989) on the basis of three specimens from Jebel Rawdah, Oman. It differs from *V. tataosi* Cotteau & Gauthier, from a similar horizon in southern Iran, by being more elongate and pointed posteriorly, and by having a smaller, more transversely elongate mouth (if the original figures of this species are true to life). The Iran species was, however, based on a single individual 27 mm in test length, and there is the possibility that with more material the two species may eventually prove to be synonymous.

Family **FAUJASIIDAE** Lambert, 1905
Genus *FAUJASIA* d'Orbigny, 1856

TYPE SPECIES. *Pygurus apicalis* Desor, by subsequent designation of Lambert & Thièry, 1921: 273.

OTHER SPECIES INCLUDED. Only one other species, *Faujasia eccentripora* Lees. Two species previously ascribed to *Faujasia* were transferred to other genera by Kier (1962): *F. faujasi* (Desmoulins) to *Eurypetalum* and *F. chelonium* Cooke to *Domechinus*.

DIAGNOSIS. Small ovoid cassiduloids with a monobasal apical disc in which the genital pores open through interambulacral plates. Petals broad, closed distally and strongly petaloid in form. Periproct small, circular and inframarginal. Peristome small, anterior with short, arcuate phyllodes in two columns and with buccal pores, and strongly projecting bourrelets.

OCCURRENCE. Maastrichtian of Belgium, France, Oman and the United Arab Emirates.

REMARKS. Kier (1962: 137), in discussing this genus, was uncertain whether *F. eccentripora* Lees truly belonged here, since its apical disc plating had never been described. As shown below, this species has an identical arrangement of gonopores opening within the adapical portion of the interambulacra as characterizes *F. apicalis* Desor and thus is clearly closely related. The derived position of gonopores outside apical disc plating distinguishes these two species from all other cassiduloids.
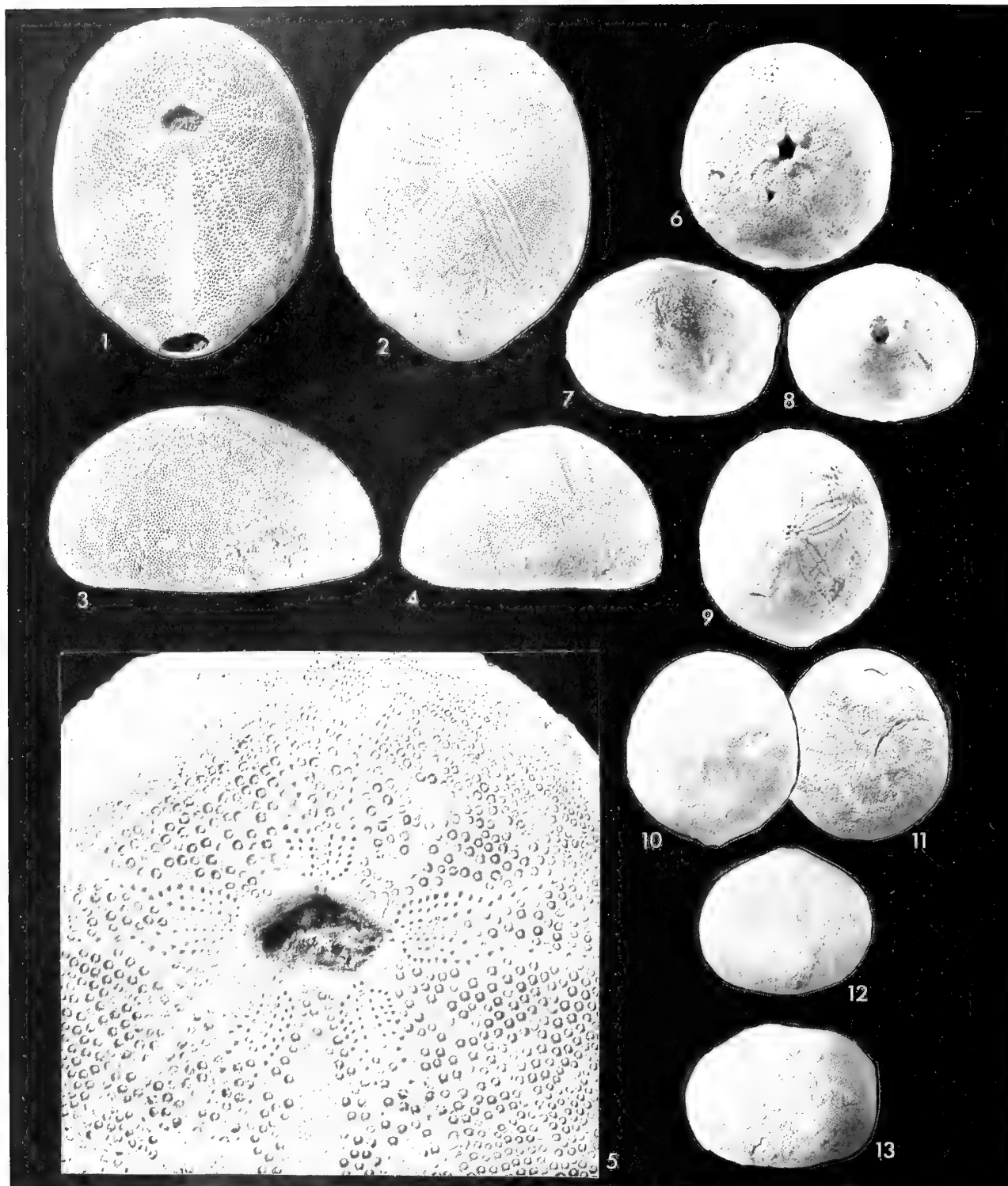
PLATE 21

Figs 1–5 *Vologesia rawdahensis* Ali. **1–3, 5,** BMNH EE4326; **1**, oral, × 1; **2**, apical, × 1; **3**, lateral, × 1; **5**, detail of peristomial region, ×
2·5. Jebel Thanais, lowest 2 m of the Simsima Formation. **4,** BMNH EE4329, lateral, × 1. Jebel Buhays, section 1; loose in the scree
derived from the lowest 3 m of the Simsima Formation.

Figs 6–13 *Zuffardia morgani* (Cotteau & Gauthier). **6–8,** BMNH EE3789; **6**, oral; **7**, lateral; **8**, posterior, all × 2. Jebel Rawdah, section 2,
bed 11. **9,** BMNH EE3791; apical, × 2. Jebel Rawdah, section 2, bed 21. **10–13,** Topotype specimen in the Morgan Collection, Museum
d'Histoire Naturelle, Paris; **10**, apical; **11**, oral; **12**, posterior; **13**, lateral; all × 1·5. Senonian, Dah-e-Rouh Davl, Iran.
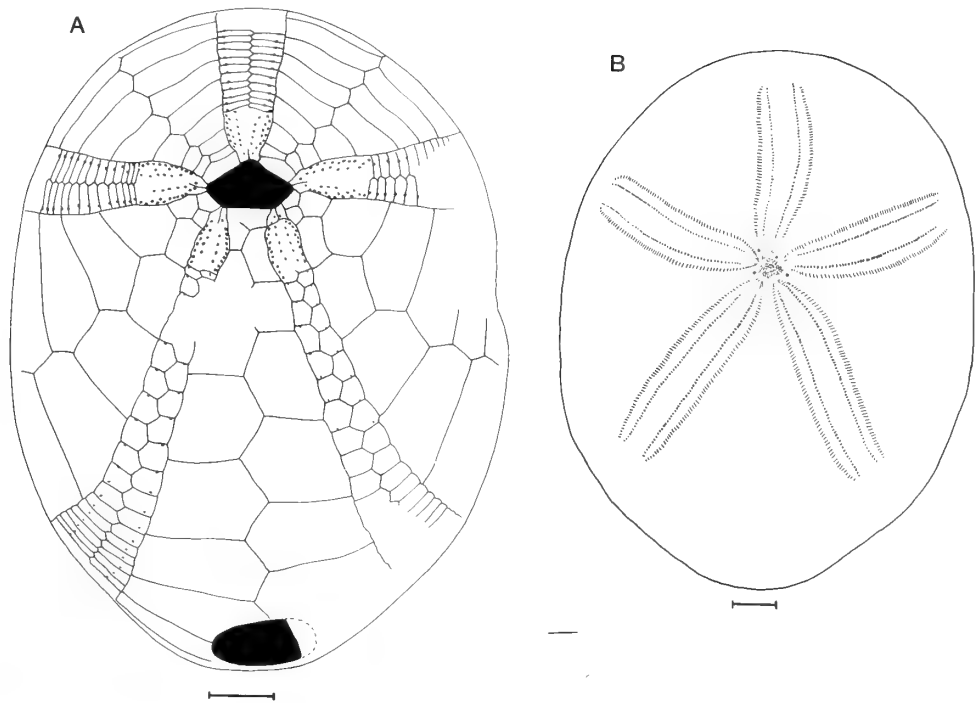
Fig. 50 Camera lucida drawings of *Vologesia rawdahensis* Ali. **A**, oral plating, BMNH EE3384; **B,** adapical plating, BMNH EE4326. Scale bars = 5 mm.
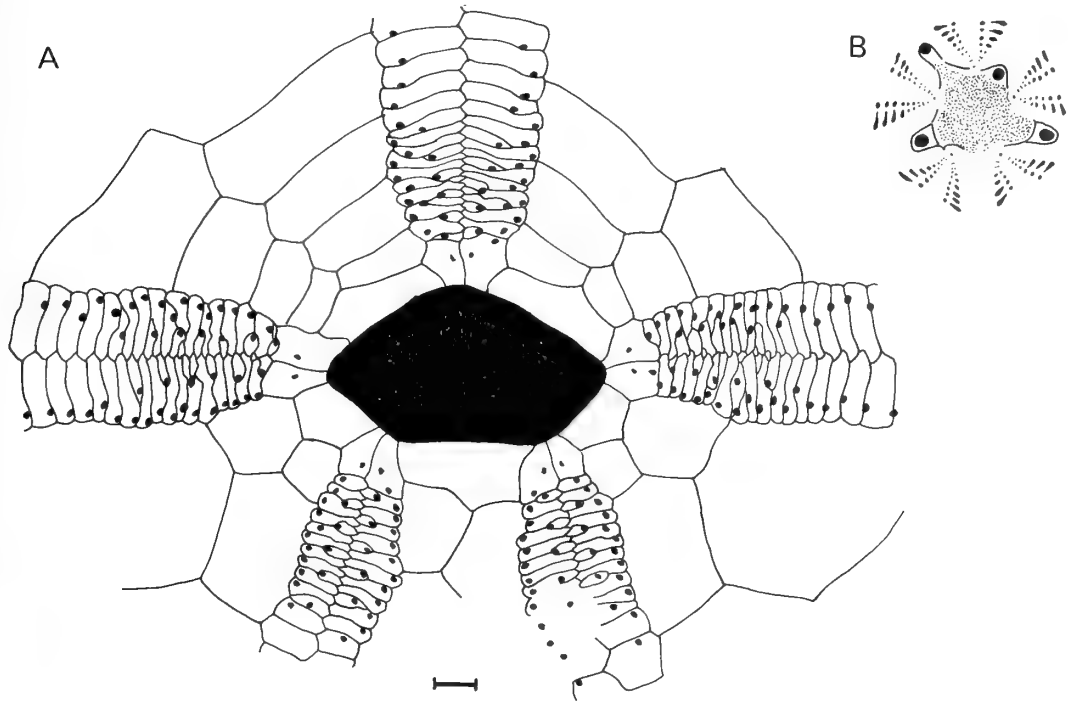
Fig. 51 Camera lucida drawings of *Vologesia rawdahensis* Ali. **A**, peristome and surrounding phyllodes, BMNH EE3384; **B,** apical disc plating, BMNH EE4326. Scale bar 1 mm.
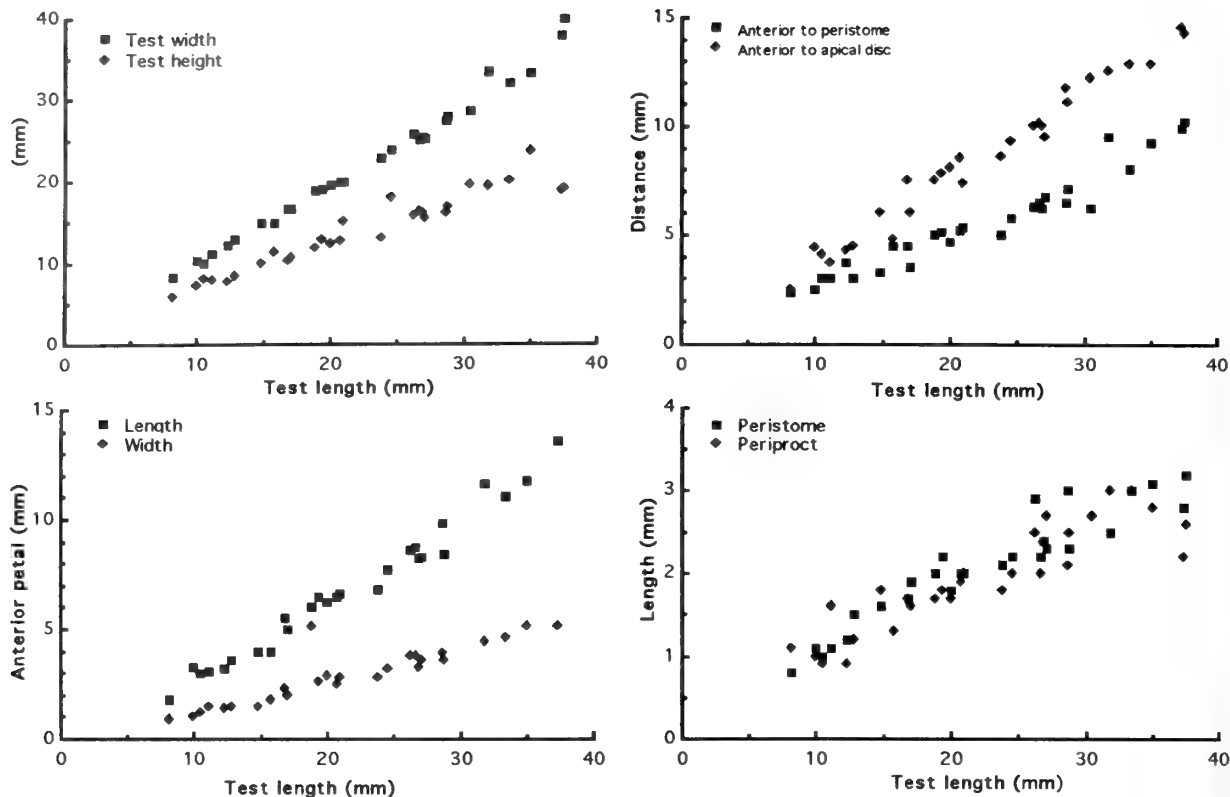
Fig. 52 Biometric data for *Faujasia eccentripora* Lees.

Faujasia eccentripora Lees, 1928   Pl. 22, figs 5–14; Figs 52–55

1928   *Faujasia eccentripora* Lees: 661, pl. 46, fig. 2.
1989   *Faujasia eccentripora* Lees; Ali: 403, fig. 4 (25).

TYPES. Holotype, BMNH E18347, paratypes BMNH E18344–46, E18348, from the late Cretaceous (?Maastrichtian) of Jebel el Malih, Oman.

MATERIAL STUDIED. 465 specimens were collected for study, of which 29 (BMNH EE3823, EE3825–26, EE3832–34, EE3836–39, EE3851, EE3855–61, EE3866–67, EE3872–76, EE3878–79, EE3882, EE3897) were measured for the biometric analysis given here.

OCCURRENCE. This species is known only from Oman and the United Arab Emirates. It occurs abundantly at the *Loftusia* levels at Jebel Huwayyah and in the lowest 8 m of calcarenitic limestones at Jebel Rawdah 2. Elsewhere it is rare. It was collected at the following localities and stratigraphic levels:
Jebel Aqabah: bed 1 (6, all juvenile).
Jebel Huwayyah, section 1: bed 9 (6); beds 10–11 (33).
Jebel Huwayyah, section 2: bed 3 (1).
Jebel Rawdah, section 1: top of bed 2 (5); top of bed 4 (2); loose in scree at base (6).
Jebel Rawdah, section 2: bed 4 (14); bed 5 (2); beds 6–8 (92); bed 10 (1); bed 11 (101); bed 14 (7); bed 16 (3); bed 19 (19); bed 20 (2); bed 21 (22); bed 22 (3); beds 23–25 (1); bed 25 (3); loose, from lower part of succession (beds 2–11) (112); loose in scree from higher part of succession (13).

Jebel Rawdah, section 3b: bed 2 (3); bed 8 (1); bed 9 (3).
Jebel Rawdah, section 4: bed 2 (1); bed 4 (2); beds 21–22 (1).

DESCRIPTION. Tests are shield-shaped in outline with a rounded anterior, a projecting pointed posterior and two marked angles coinciding with the posterior ambulacra (Pl. 22, figs 5–14; Fig. 53). Tests range in length from 8 to 37·5 mm. They have a rounded ambitus and slightly convex oral surface, with a marked sternal keel. The test is widest posterior of midlength and maximum width is 92–106% test length. The upper surface is low and rounded, never peaked. Test height is 50–77% of test length, being greatest in small individuals and progressively decreasing through growth (Fig. 52).

The apical disc lies 30–44% of test length from the anterior border (mean = 38%, N = 29). It is more central in larger forms. The disc is monobasal with the entire apical region occupied by the madreporite. There are four gonopores but these lie outside the apical disc, opening instead within the interambulacra and separated from the madreporite by one or two interambulacral plates (Fig. 54).

The petals are strongly inflated and closed distally, being widest at midlength (Pl. 22, figs 6, 10, 13; Fig. 53B). All five are similar in size and the anterior three extend some 70–80% of the way from the apex to the ambitus. Both pores in the pore-pair are circular or subcircular and united by a furrow. Pores are all single beneath the petals.

The peristome is small, only about 10% of the test length in diameter. It is rounded quinquestellate in outline and approximately as wide as broad. It lies 20–30% of the test length from the anterior border (mean = 25%, N = 29). The
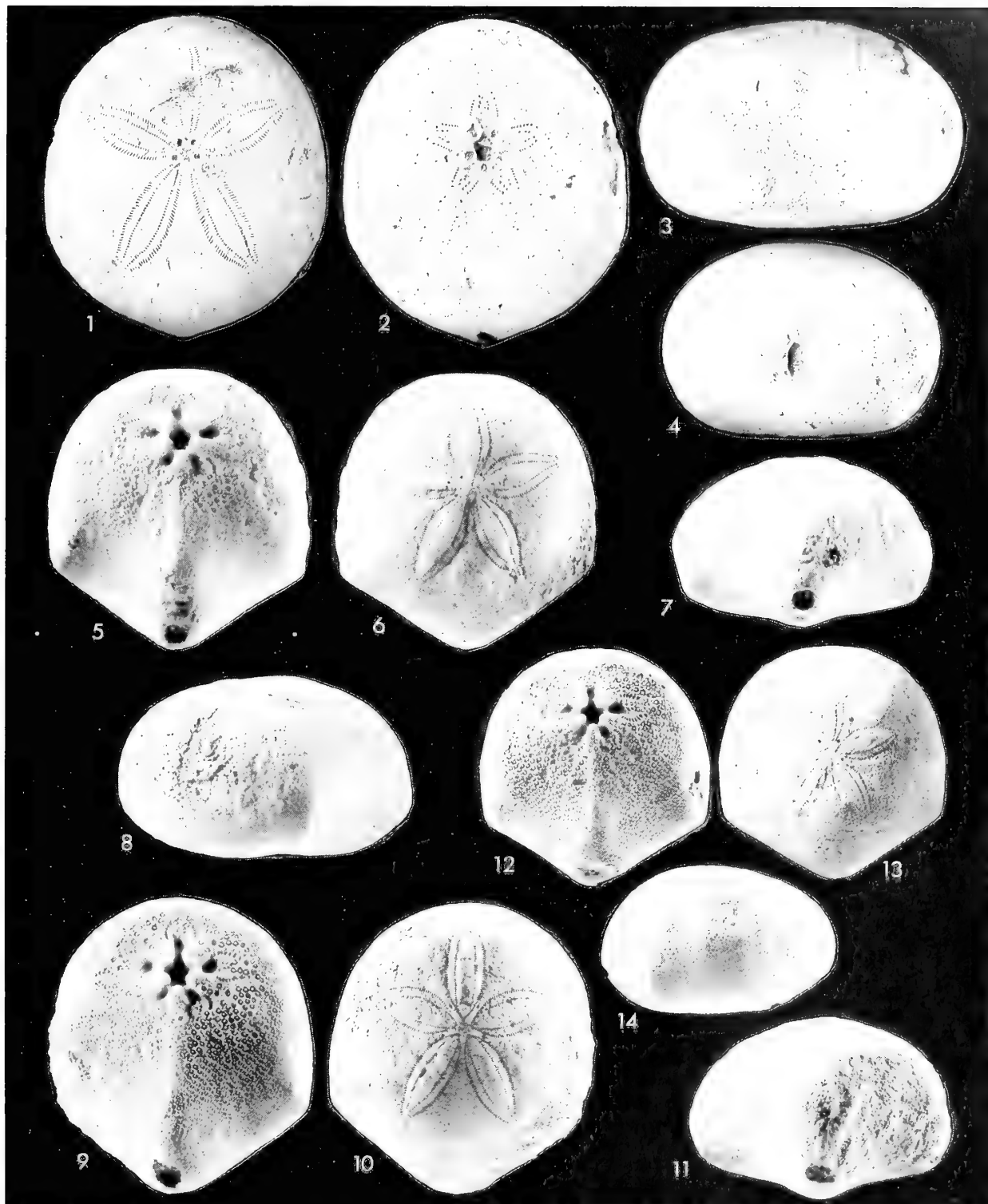
PLATE 22

Figs 1–4 *Zuffardia morgani* (Cotteau & Gauthier). BMNH EE4325; **1**, apical; **2**, oral; **3**, lateral; **4**, posterior; all × 2. Jebel Rawdah, section 1, bed 3.

Figs 5–14 *Faujasia eccentripora* Lees. **5–7,** BMNH EE3821; **5**, oral; **6**, apical; **7**, posterior; all × 2. Jebel Rawdah, section 2, bed 14. **8–11,** BMNH EE3826; **8**, lateral; **9**, oral; **10**, apical; **11**, posterior; all × 2. Jebel Rawdah, section 2, loose in scree at level of bed 14. **12–14,** BMNH EE3825; **12**, oral; **13**, apical; **14**, lateral; all × 2. Jebel Rawdah, section 2, bed 11.
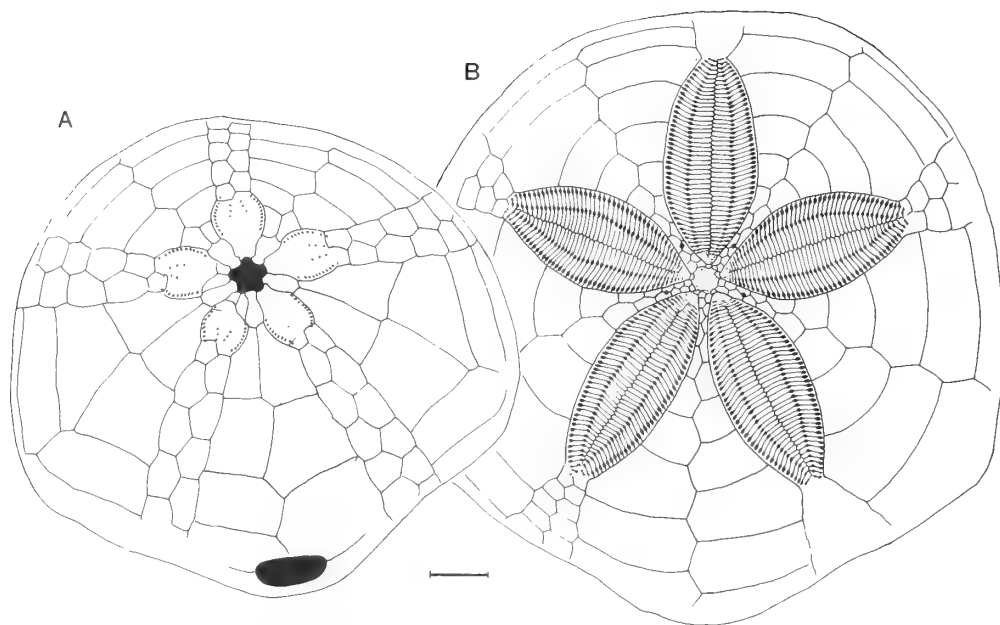
Fig. 53 Camera lucida drawings of *Faujasia eccentripora* Lees. **A**, BMNH EE3882, oral surface; **B**, BMNH EE3824, adapical surface. Scale bar = 5 mm.

basicoronal plates of the interambulacra are rather narrow and elongate (Fig. 55), as are the next two pairs of plates in the posterior three interambulacra (Fig. 54). The bourrelets are rather square-sided and blunt-ended and project strongly (Pl. 22, figs 5, 9, 12). The phyllodes are short and broad and are sunken. Pores are strongly arcuate with 8 to 12 pores in the outer series and only 2 or 3 in the inner series (Fig. 55). The inner series of pores are well separated from the peristome, but there are two pairs of sphaeridial pits adorally (Fig. 55). Miniscule buccal pores are present but are much smaller than other pores in the phyllodes and are clearly rudimentary only.

The periproct is small and circular, width being 85–122% of its length. It lies close to the posterior margin on the oral surface at the end of the sternal ridge and faces slightly posteriorly (Pl. 22, figs 7, 11).

Tuberculation is fine and uniform aborally and slightly coarser adorally. There is a narrow naked zone that extends from just posterior of the posterior bourrelet half way towards the periproct.

REMARKS. This species was first erected by Lees (1928) for specimens from Jebel el Malih, Oman. It differs from *Faujasia apicalis* Desor, from the Maastrichtian of Belgium, the Netherlands and France in a number of important respects. *F. apicalis* has shorter petals, a sharper ambitus and is more pointed apically in profile. Furthermore, its peristome is much less anterior and the oral surface is flatter and lacks such a pronounced sternal keel.

Genus *ZUFFARDIA* Checchia-Rispoli, 1917

TYPE SPECIES. *Pseudocatopygus sanfilippoi* Checchia-Rispoli, 1914, by original designation.

OTHER SPECIES INCLUDED. In addition to the type species, there are four nominal species, three of which have previ-
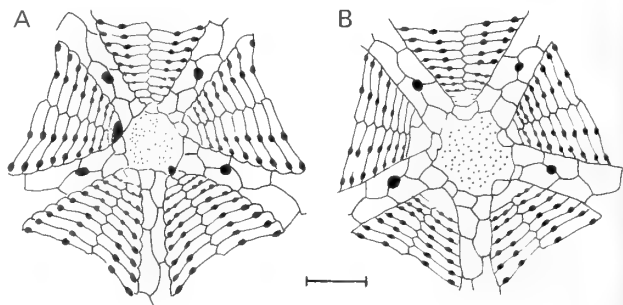
Fig. 54 Camera lucida drawings of apical disc plating of *Faujasia eccentripora* Lees. **A**, BMNH EE3824; **B**, BMNH EE3826. Scale bar = 1 mm.
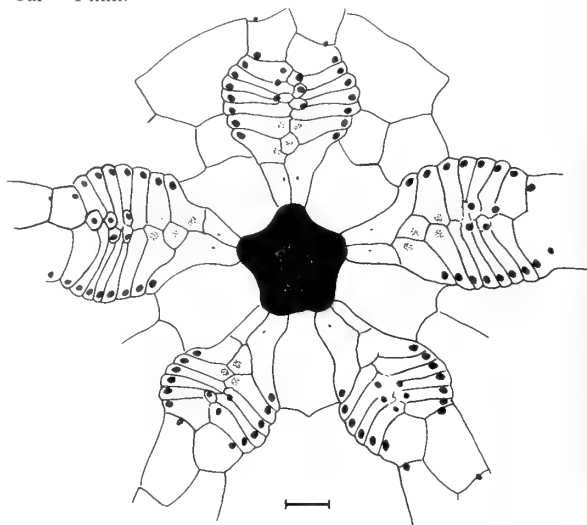
Fig. 55 Camera lucida drawing of phyllode plating in *Faujasia eccentripora* Lees, BMNH EE3902. Scale bar = 1 mm.
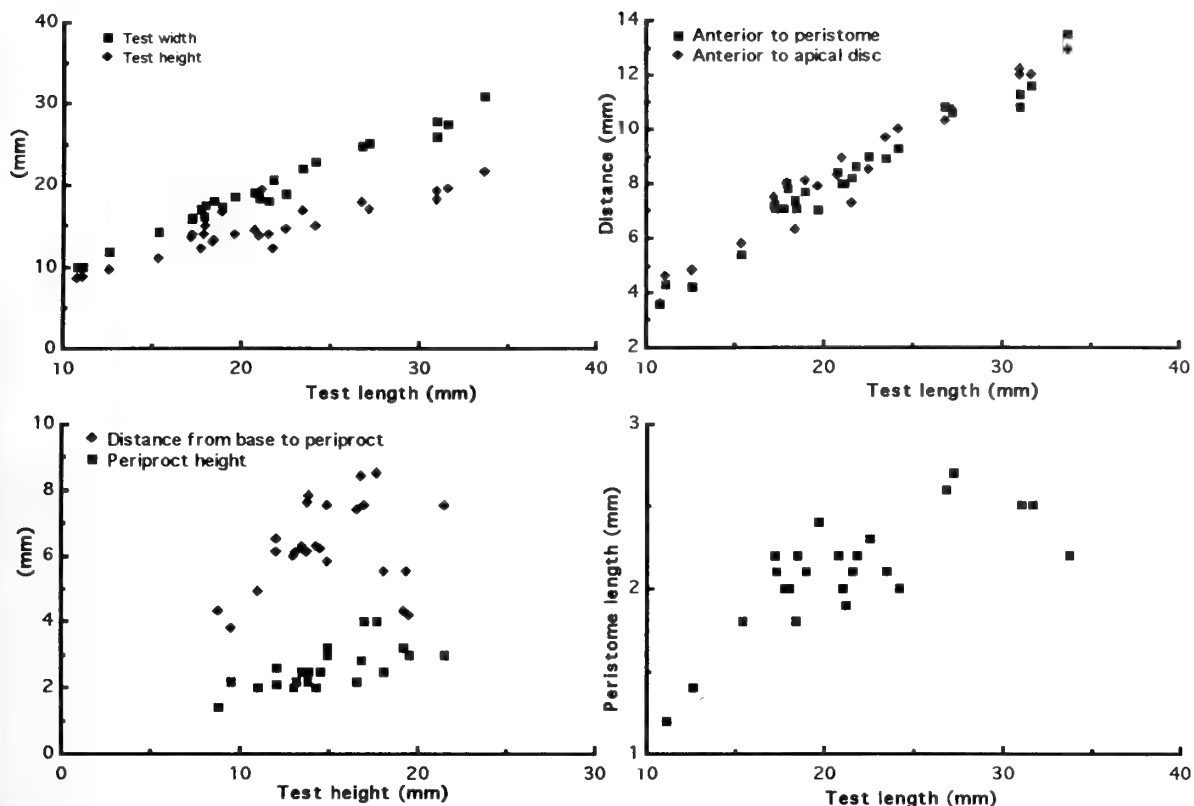
Fig. 56 Biometric data for *Zuffardia morgani* (Cotteau & Gauthier).

ously been assigned to this genus; *Catopygus rohlfsi* Krumbeck, 1906, *Catopygus boucarti* Lambert & Thièry, 1925, *Catopygus morgani* Peron & Gauthier, 1895, *Zuffardia creullii* Checchia-Rispoli, 1933. All are here treated as synonymous with *C. morgani*, the oldest available name.

DIAGNOSIS. Oval test with a monobasal apical disc, broad petals of equal length, a posterior longitudinal periproct and a longitudinal peristome with short phyllodes and buccal pores.

OCCURRENCE. The genus occurs in the late Cretaceous of North Africa and the Middle East. It is recorded from the Maastrichtian of Libya, Algeria and Oman and the United Arab Emirates, and from the upper Senonian (?Maastrichtian) of southern Iran.

REMARKS. This genus resembles *Catopygus* Agassiz, 1836, in its general shape and form but differs from that genus in having a monobasal apical disc and single pores below the petals. It also appears rather similar to the Tertiary genus *Kephrenia* Fourtau, 1909, having very similar phyllodes and longitudinal peristome. It differs from *Kephrenia* in periproct shape, *Kephrenia* having a small transverse periproct as opposed to the longitudinal periproct of *Zuffardia*. It also shares many characteristics in common with *Faujasia*, including its phyllode and bourrelet structure, small periproct positioned low on the posterior face and apical disc plating. It differs from *Faujasia* in having gonopores confined to genital plates, and in being much more oval in shape.

Only two species are recognized here, the type *Z. sanfilippoi* and *Z. morgani* (Cotteau & Gauthier).

Zuffardia morgani (Cotteau & Gauthier, 1895) Pl. 21, figs 6–13; Pl. 22, figs 1–4; Figs 56–59

1895 *Pseudocatopygus Morgani* Cotteau & Gauthier: 60, pl. 9, figs 6–9.
?1906 *Catopygus Rohlfsi* Krumbeck: 87, pl. 7, fig. 4.
1914 *Pseudocatopygus rohlfsi* Krumbeck; Checchia-Rispoli: 301, pl. 1, fig. 3.
1925 *Catopygus boucarti* Lambert; Lambert & Thièry: 587, pl. 13, figs 6–9.
1933 *Zuffardia creullii* Checchia-Rispoli: 4, pl. 1, figs 1–4.
1939 *Catopygus boucarti* Airaghi: 258.
1981 *Zuffardia rohlfsi boucarti* (Lambert); Roman, in Amard *et al.*: 112.
1987 *Zuffardia* aff. *rohlfsi boucarti* (Lambert); Zhagbib-Turki: 257.
1989 *Zuffardia sanfilippoi* Ali: 406, fig. 5 (67).

TYPES. The holotype is the single specimen figured and described by Cotteau & Gauthier (1895). It has not been located. However, another specimen from the same locality and in the Morgan collection is figured here (Pl. 21, figs 10–13).

MATERIAL STUDIED. Seventy one specimens were collected, of which 28 (BMNH EE3382–85, EE3531, EE3789–93, EE3796–804, EE3806, EE3808, EE3812–17, EE4325, EE5050) were used for the following biometric analysis.

OCCURRENCE. The species occurs In Tunisia, Algeria and Libya as well as in southern Iran and the United Arab Emirates and Oman. It is apparently restricted to the Maas-
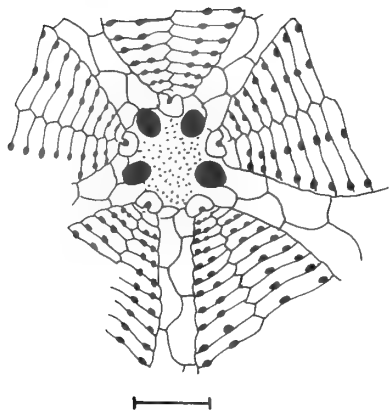
Fig. 57 Camera lucida drawing of apical disc plating in *Zuffardia morgani* (Cotteau & Gauthier), BMNH EE3791. Scale bar = 1 mm.

trichtian. In the study area described here, the species is found only at Jebel Rawdah, at the following localities:

Jebel Rawdah, section 1: bed 3 (5).

Jebel Rawdah, section 2: bed 11 (47); bed 19 (5); bed 21 (5); bed 25 (1); loose, mostly derived from beds 2–11 (48).

Jebel Rawdah, section 4: bed 2 (1).

DIAGNOSIS. A species of *Zuffardia* with a rather flat base and a periproct that becomes progressively more adoral as test size increases. Test shape highly variable, either inflated, keeled or depressed.

DESCRIPTION. Tests ovoid in shape ranging from 10·8 to 33·7 mm in length. In plan view they are rounded anteriorly and slightly pointed posteriorly (Pl. 21, fig. 9). The ambitus is

rounded and in profile the base is flattish and the upper surface ranges from low-domal or even flat, to conical and pointed at the apex (Pl. 21, fig. 7; Pl. 22, fig. 3). Test width is 83–97% of the length (mean = 90%, N = 25) and test height 55–91% of the length (mean = 71%, smaller individuals being proportionately taller, Fig. 57).

The apical disc is monobasal and positioned 33–47% of the test length from the anterior border (mean = 40%, N = 24; Fig. 56). The madreporite is large and its pores extend to, and partially enclose, the four gonopores (Fig. 57). There appears to be a distinct sexual dimorphism in gonopore size, with large individuals having either large, closely spaced gonopores some 0·3–0·5 mm in diameter (female?) and others of comparable size having only small (0·1 mm diameter) gonopores (male?).

Petals are lanceolate and converge distally but do not close (Pl. 22, fig. 1; Fig. 58B). Petals II, III and IV are about 70–80% the length of the posterior petals. The two pores in each pair are approximately circular and connected by a groove. The three anterior petals extend approximately 70% of the distance to the ambitus, the posterior pair only some 60% or so. In middle to large individuals the interporal zone is 1·0–1·5 times as broad as an individual pore zone. Pores below the petals are all single.

The peristome is pentagonal in outline and slightly longer than wide (length is 1·2–1·5 times its width; mean = 1·3). It lies 33–38% of test length from the anterior border. Phyllodes are short and arcuate, with two series of pores in each column (Fig. 59). There are 6 or 7 pores in the outer series and only 1 or 2 in the inner series. There are also two pairs of sphaeridial pits in each half ambulacrum situated perradially. A small number of occluded plates are developed and buccal pores are present. The phyllodes are not depressed but remain flush with the test. The bourrelets project outwards strongly but do not indent the peristome (Pl. 21, fig. 6; Pl. 22, fig. 2).
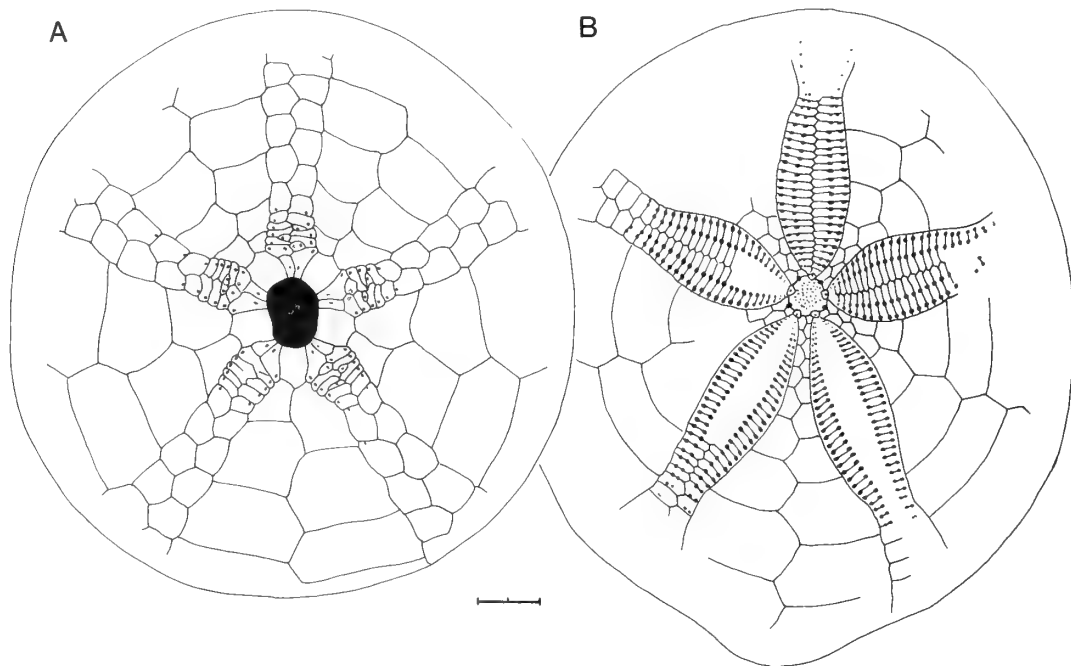
Fig. 58 Camera lucida drawings of plating in *Zuffardia morgani* (Cotteau & Gauthier). **A,** BMNH EE3385, oral plating; **B,** BMNH EE3384, adapical plating. Scale bar = 2 mm.

The periproct lies on the posterior face, relatively high in juveniles but becoming progressively lower in larger specimens (Fig. 56). The base of the periproct lies 50% of test height above the base in small individuals, but can lie as low as 22% of test height in the largest individuals. There is, however, considerable variation in the height of the periproct within the sample. The periproct is relatively small and taller than wide (height = 1·3–2·5 times greater than width). Typically, there is a slight adapical projection and rim developed around the periproct.

Tuberculation is fine and uniform aborally and slightly coarser adorally. There is a narrow sternal naked zone on the oral surface behind the peristome.

REMARKS. This species was first described from the 'Upper Senonian' (probably Maastrichtian) of Derre-i-Chahr, southern Iran, by Cotteau & Gauthier (1895: 60) under the name *Catopygus morgani*. Cotteau & Gauthier distinguished it from other similar species by its inflated shape and convex oral surface. Although their figure indicates a peristome that is as broad as long, in all other respects it falls exactly within the range of the United Arab Emirates population described here (Fig. 57). Should the Iranian population prove to have a consistently more equant peristome, then it clearly should be treated as a distinct species. However, the figures cannot be considered entirely reliable and this difference is not apparent in topotype material (Pl. 21, figs 10–13). Consequently, for the present the two forms are synonymized.

In 1906 Krumbeck erected the species *Catopygus rohlfsi* on the basis of a specimen from the late Cretaceous of Libya. Closely comparable material from Algeria was given the name *Catopygus boucarti* by Lambert & Thièry (1925). Based on a large collection of specimens from the Maastrichtian of Libya, Airaghi (1939) was later able to synonymize Lambert's *Catopygus boucarti* and Krumbeck's *Catopygus rohlfsi*. The large populations of *Zuffardia boucarti* Lambert, described from Algeria by Roman (in Amard *et al.* 1981) also fall within the range of the material described here, though they do not achieve a size greater than about 2 cm (Libyan specimens cover an identical range to the population described here).
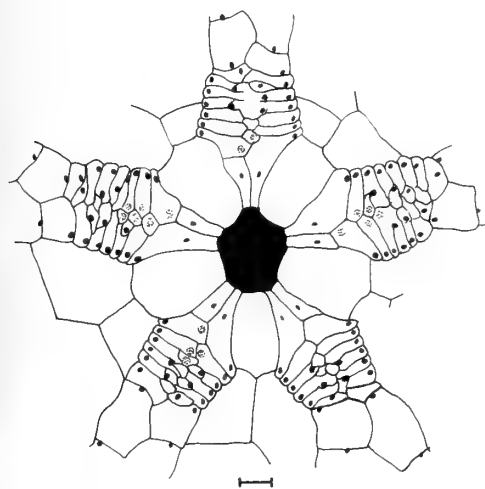
Fig. 59 Camera lucida drawing of adoral plating of *Zuffardia morgani* (Cotteau & Gauthier), BMNH EE4325. Scale bar = 1 mm.

Thus there can be little doubt that these populations are all synonymous. However, there remains slight doubt over whether Krumbeck's original specimen is conspecific. Roman (in Amard *et al.* 1981) pointed out that Krumbeck's (1906) original figure shows a specimen whose apical disc lies well displaced towards the anterior and whose periproct is shown as being visible from above. I suspect that this is simply due to the Krumbeck's specimen being slightly crushed and distorted, or possibly simply being illustrated from an oblique angle. But the type specimen has not been located and thus the validity of this species must remain uncertain.

In 1914 Checchia-Rispoli described a more spherical form with a strongly inflated oral surface under the name *Pseudocatopygus sanfilippoi*. There are three specimens, the largest of which is 42 mm in length. This form has a much higher periproct than is found in my populations (Fig. 57), and corresponds to the juvenile positioning (as does the more spherical test shape). This lies well outside the range of form found in *Z. morgani* from either the Algerian or the United Arab Emirates populations, and clearly represents a distinct species. Checchia-Rispoli (1917) made this the type species of his new genus *Zuffardia*.

The only other species assigned to *Zuffardia* is *Z. creullii* Checcia-Rispoli (1933). This is based on a single individual 33 mm in length that corresponds to a more inflated variant of *Z. morgani*. Biometrically it falls more or less within the range of variation encountered in the population described here. It too, therefore, is synonymized with *Z. morgani*.

Unnamed Family
Genus *PYGUROSTOMA* Cotteau & Gauthier, 1895

TYPE SPECIES. *Pygurostoma morgani* Cotteau & Gauthier, 1895, by original designation.

OTHER SPECIES INCLUDED. None.

OCCURRENCE. Late Cretaceous of Iran and the Oman Mountains.

DIAGNOSIS. Large, oval and rather flattened cassiduloid with a narrow, elongate and invaginated inframarginal periproct. Peristome quinquestellate and subcentral with strong phyllodes containing many occluded plates and pores. Buccal pores present, well separated from the peristome. Apical disc tetrabasal and subcentral. Petals long and well developed, converging distally. Naked zone on the oral area between the peristome and periproct, and also extending anterior of the peristome in ambulacrum III.

REMARKS. Kier (1962) included *Pygurostoma* in the family Faujasiidae on account of its phyllode structure. However, as Kier pointed out, this genus is rather different from other Faujasiidae. In particular the appearance of the periproct, which is strongly rostrate adapically and invaginated adorally, indicates that it is probably derived from a form with a posterior elongate periproct and weak anal canal. This is very different from the periproct seen in *Faujasia* and most other faujasiids. In test shape, peristome position and size, floscelle development, petal form and the distribution of naked zones, *Pygurostoma* undoubtedly comes closest to *Parapygus* Pomel, 1883. *Parapygus* has a narrow, vertically elongate periproct that lies posteriorly and in large forms is just visible adorally. Although many species have just two columns of pores in each half ambulacrum of the phyllodes, the type

species, *P. cotteauanus* (d'Orbigny) has a median zone of pores also. Thus, in many respects *Pygurostoma* is no more than an hypertrophic form of *Parapygus* in which the phyllodes have increased numbers of median pores and the periproct is inframarginal rather than marginal.

Only one other species was included in this genus by Kier (1962), *Pygurostoma pasionensis* Cooke, 1949, from the late Cretaceous of Guatemala. However, this species has its periproct flush with the test and not invaginated. I suspect this is not cogeneric.

Pygurostoma morgani Cotteau & Gauthier, 1895 Pl. 23, figs 1–4, 7; Figs 60–63

1895 *Pygurostoma morgani* Cotteau & Gauthier: 52, pl. 8, figs 1–5.
1962 *Pygurostoma morgani* Cotteau & Gauthier; Kier: 135, pl. 19, figs 1–3, text–fig. 117.
1992 *Pygurostoma morgani* Cotteau & Gauthier; Ali: 72, fig. 4.

TYPES. The whereabouts of Cotteau & Gauthier's specimens is unknown. A topotype specimen from the Morgan collection is illustrated (Pl. 23, fig. 1).

MATERIAL STUDIED. Forty specimens, of which 15 (BMNH EE3291–92, EE3296, EE3302–10, EE3315, EE3317, EE3322) were measured.

OCCURRENCE. The species was first described from the 'Upper Senonian' of Aftab, Louristan, southern Iran. In this study specimens were most common in the lowest few metres of the Simsima limestones. Fifty specimens were collected or noted at the following localities and horizons:

Jebel Buhays, section 1: loose in the scree, derived from the lowest few metres of Simsima Formation (26).
Jebel Buhays, section 2: loose in scree, derived from lowest 2 m of the Simsima Formation (2).
Jebel Thanais: lowest 2 m of Simsima Formation (1).
Jebel Huwayyah, section 1: beds 14/15 (3).
Jebel Rawdah, section 2: bed 14 (3); bed 18 (1); bed 19 (2); bed 21 (7); bed 26 (2); loose in scree (1).
Jebel Rawdah, section 4: bed 19 (1).
Jebel Faiyah, section 1 (southern tip): bed 8 (1).

DIAGNOSIS. As for genus.

DESCRIPTION. Tests are oval in outline with a rounded anterior and slightly pointed and projecting posterior (Pl. 23, figs 1–3). In profile the test is low domal with a rounded ambitus and slightly angled posterior (Pl. 23, fig. 4). The oral surface is concave towards the peristome. Test length ranges from 55 to 95 mm. Test width is 65–81% of test length (mean = 76%, N = 15), test height 35–47% of test length (mean = 40%).

The apical disc lies 37–44% of test length from the anterior border. It is tetrabasal (Fig. 62), with genital plates 1, 2 and 4 reduced to minute plates largely occupied by the gonopores. The madreporite is stellate in form.

Petals are long and weakly lanceolate in outline (Fig. 61). The anterior petal and the two posterior petals are similar in length, being 35–42% of the test length. The latero-anterior petals are shorter, typically 80–90% of the length of the other
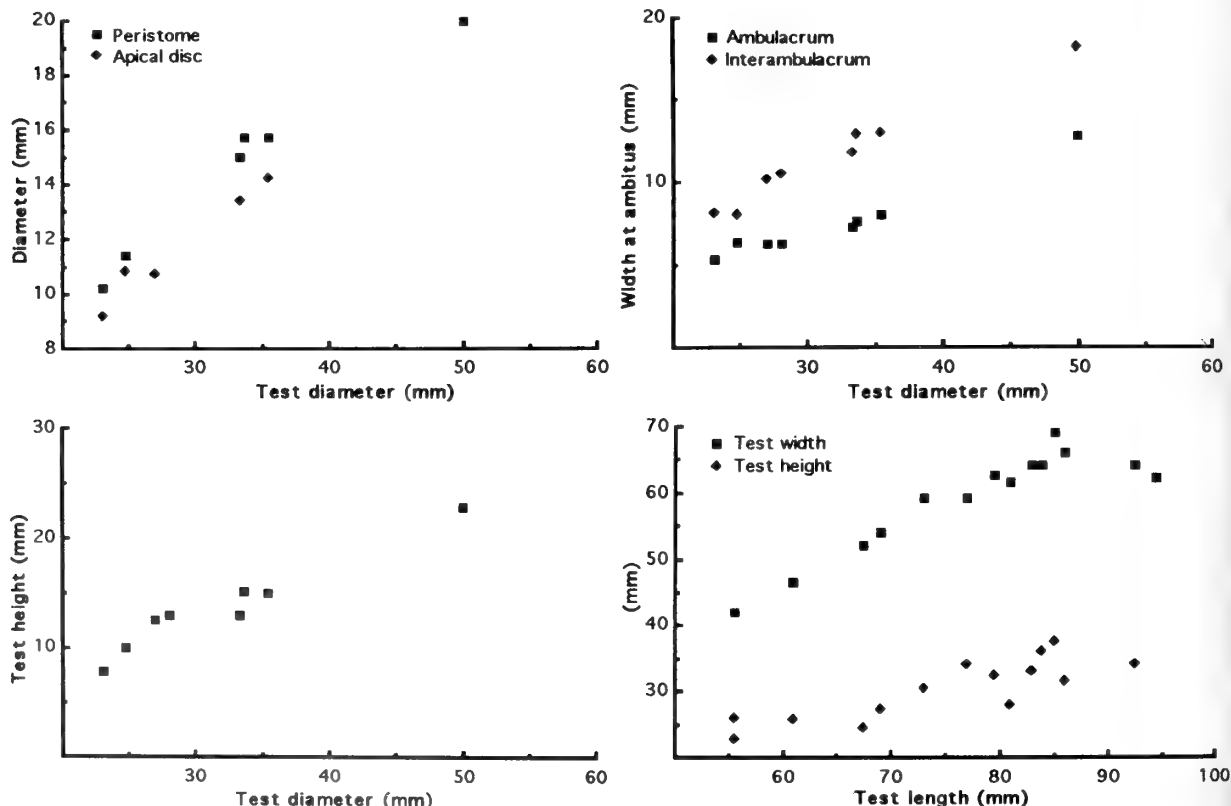
Fig. 60 Biometric data for *Pygurostoma morgani* Cotteau & Gauthier.
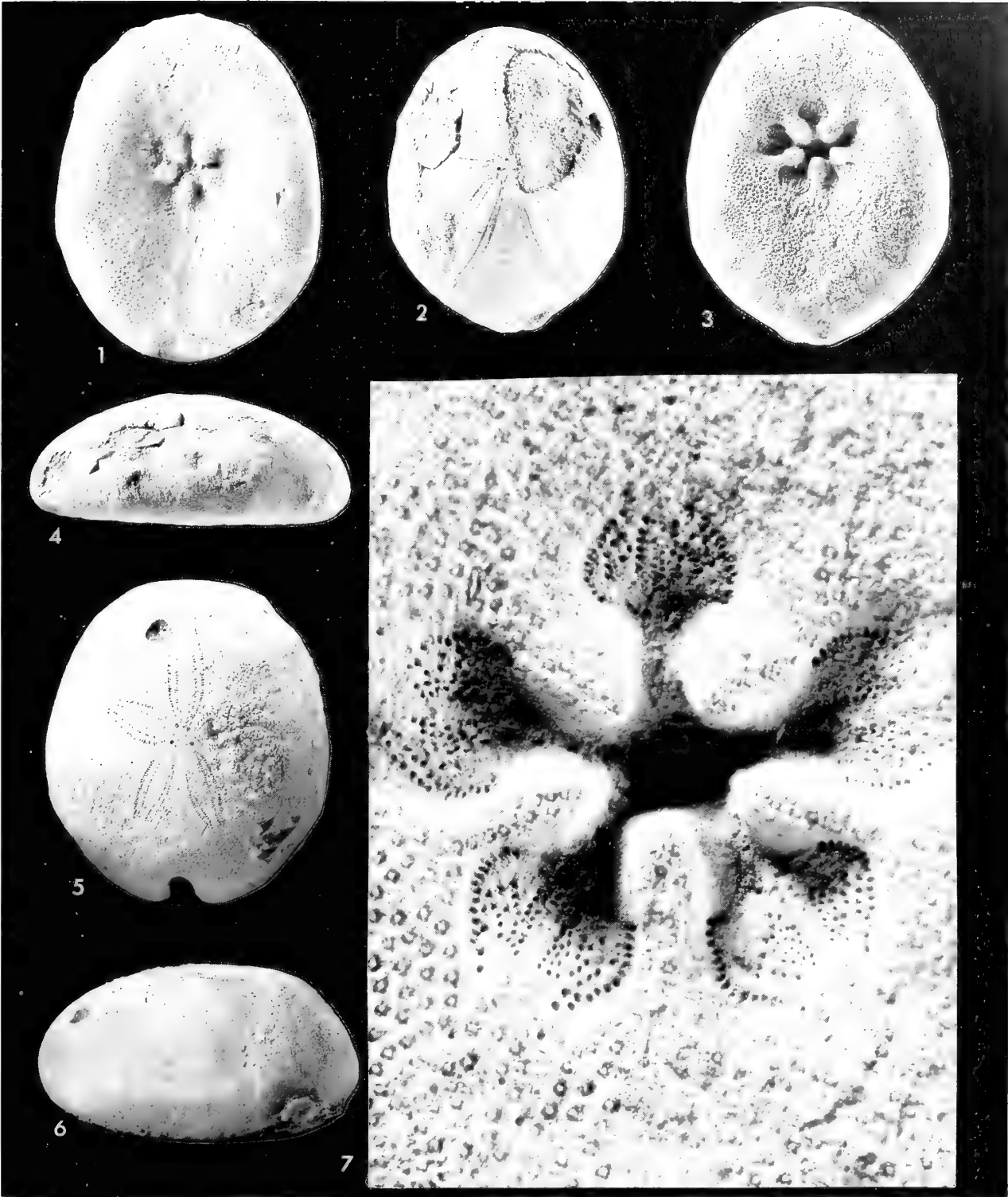
PLATE 23

Figs 1–4, 7 *Pygurostoma morgani* Cotteau & Gauthier. **1,** specimen in the Morgan Collection, Museum d'Histoire Naturelle, Paris; oral, ×
1. Senonian of Iran; no locality details. **2–4, 7,** BMNH EE3315; **2,** apical, × 0·9; **3,** oral, × 1; **4,** lateral, × 1; **7,** detail of peristome × 6.
Jebel Rawdah, section 2, loose in scree at level of bed 12.

Figs 5, 6 *Petalobrissus linguiformis* (Peron & Gauthier). BMNH EE4318; **5,** apical; **6,** lateral; both × 2. Jebel Rawdah, section 2, bed 21.
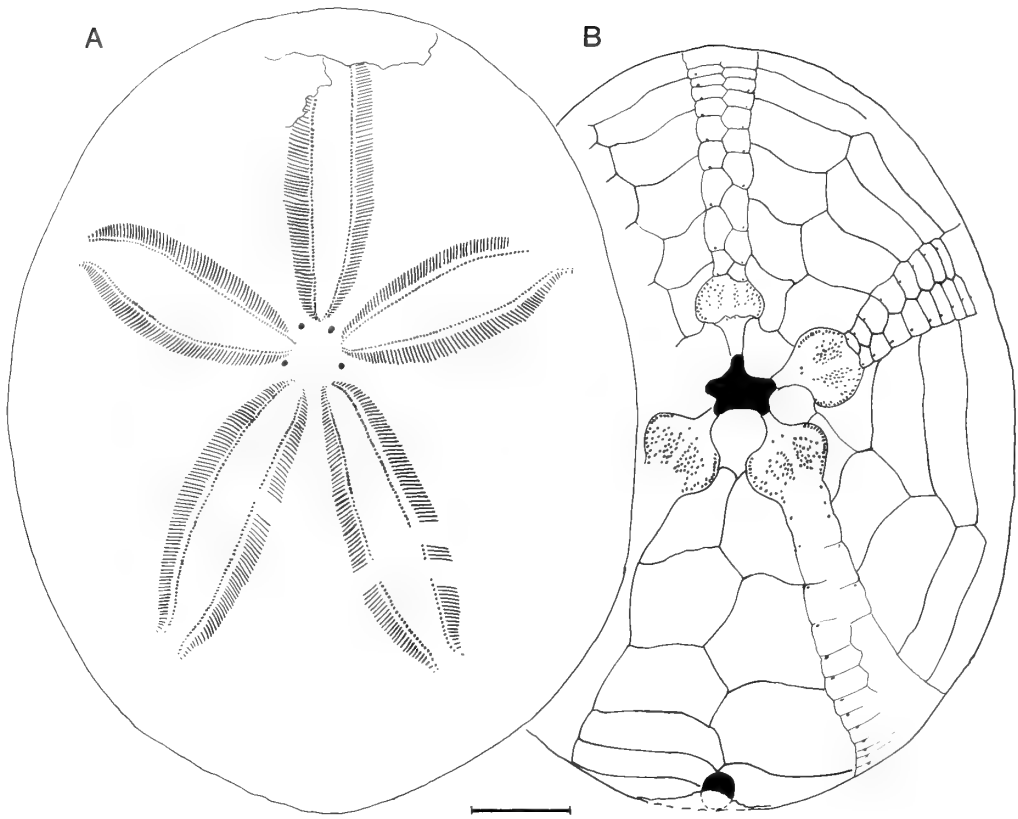
Fig. 61 Camera lucida drawings of plating in *Pygurostoma morgani* Cotteau & Gauthier. **A**, BMNH EE3303, apical; **B**, BMNH EE3304, oral. Scale bar = 1 cm.

three. The anterior petal is also typically narrower and more parallel-sided than the other petals. The two pores are subcircular and widely separated, united by a well developed groove. The petals converge slightly distally but do not close (Fig. 61). The interporal zone is about twice the width of a single pore zone. Pores below the petals are all single.

The peristome is quinquestellate in outline with the prominent bourrelets projecting into the opening (Pl. 23, fig. 7). The bourrelets are triangular and have long lateral bands of fine tuberculation. They are blunt-ended. The phyllodes are distinctly sunken and arcuate. They consist of many rows of pores (Fig. 63). There is a well defined outer series and inner series in each half ambulacrum, but the central zone consists of a broad band of unorganised pores, four or five abreast. The anterior ambulacrum, however, has notably fewer median pores than other ambulacra, with only one or two median pores abreast. There are 16–18 pores in the outer series and 7 or 8 in the inner series. There are many occluded plates in the phyllodes (Fig. 63). The peristome is 1·4 to 2·1 times as wide as it is long and is situated 33–43% of test length from the anterior border (mean = 39%, N = 13).

The peristome is small and lies inframarginally, typically forming a small pointed rostrum. There is a distinct, well-formed invagination of the test on the adoral margin of the periproct but not adambitally. The periproct is oval and longer than wide (width = 45–70% of length). It opens between interambulacral plates 6 and 8 (Fig. 61).

Tuberculation is fine and dense aborally, slightly less fine and less dense adorally. There is a very pronounced fusiform

naked zone along the sternum between the peristome and periproct. This is slightly raised above the surrounding test and is covered in small pits. There is a similar, smaller naked zone developed anterior of the peristome in ambulacrum III.

REMARKS. The species was described and figured by Cotteau & Gauthier (1895). In the same work they described a number of smaller species of *Parapygus* under the name *Pseudocatopygus*. Some of these may possibly turn out to be juveniles of *P. morgani*.

This species is very different from the only other possible species assigned to this genus, *P. pasionensis* Cooke (1949), from the ?Campanian of Guatamala. *P. pasionensis* has much less well developed bourrelets and its periproct is more equant and lies completely flush and is not invaginated. As discussed above, it is not clear that *P. pasionensis* is congeneric with *P. morgani*.

Family **CASSIDULIDAE** Agassiz & Desor, 1847
Genus *PETALOBRISSUS* Lambert, 1916

Petalobrissus rawdahensis sp. nov.   Pl. 24, figs 1–12;
Figs 64, 65

TYPES. Holotype, BMNH EE3485; paratypes, BMNH EE3467–84, EE3486–87, EE4321–22.

OTHER MATERIAL. Over 650 specimens were collected.
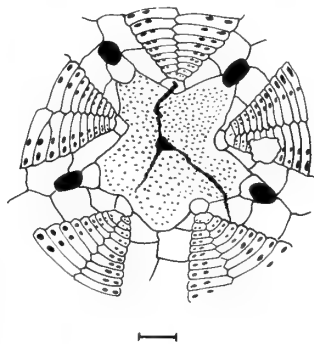
Fig. 62 Camera lucida drawing of apical disc plating in *Pygurostoma morgani* Cotteau & Gauthier, BMNH EE3288. Scale bar = 1 mm.
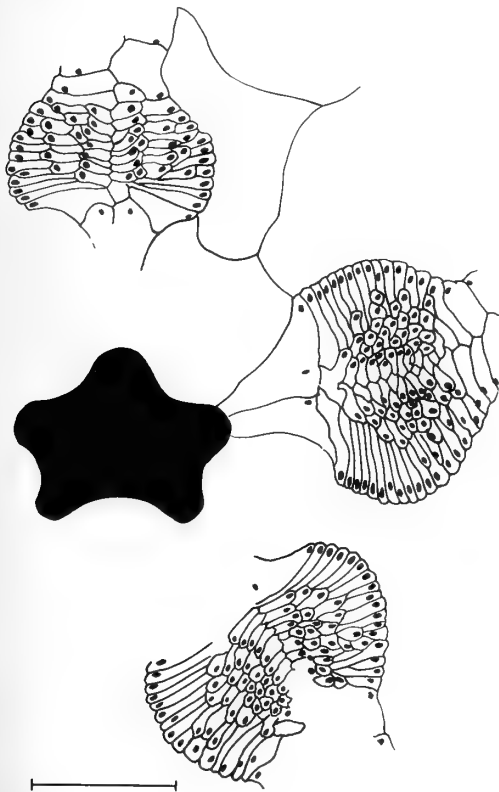
Fig. 63 Camera lucida drawing of phyllode plating in *Pygurostoma morgani* Cotteau & Gauthier, BMNH EE3304. Scale bar = 5 mm.

OCCURRENCE. This species occurs abundantly at Jebel Rawdah, section 2 but is found virtually nowhere else. The only other occurrence of this species is in the lowest bed (bed 1) at Jebel Rawdah, section 3b. At section 2 the species is found at the following levels: bed 4 (3); bed 8 (4); bed 11 (247); bed 12/13 (230); bed 14 (17); bed 15 (25); bed 19 (73); beds 20–21 (45); bed 22 (13); bed 26 (2). Additional material was collected loose from the scree at this locality.

DIAGNOSIS. A *Petalobrissus* with a monobasal apical disc and a small quinquestellate peristome, anterior in position and surrounded by small pointed bourrelets. Phyllodes well-developed, composed of outer and inner series of pores. Buccal pores present. Periproct posterior, longitudinal. Narrow, smooth tubercle-free zone present both anterior and posterior to the peristome. In outline the posterior projects slightly and adorally there is a characteristic interradial keel in the posterior interambulacrum.

DESCRIPTION. Tests are oval in outline, uniformly rounded at the anterior, but slightly pointed posteriorly (Pl. 24, figs 5, 6). Test length ranges from 10·3 to 21·2 mm. Test width is 88–95% of test length (mean = 91%, SD = 1·8%, N = 23) and the widest point is slightly posterior of midlength. In profile the test is depressed with a relatively flat upper surface, a uniformly rounded anterior and an obliquely truncated posterior (Pl. 24, figs 4, 7, 10, 11). The tallest point coincides with the apical disc or is slightly posterior to it. The ambitus is rounded and relatively low. Test height is 51–62% of test length (mean = 56%, SD = 2·4%, N = 23; Fig. 64). The oral surface is flat anteriorly, but slopes away towards the posterior. There is a relatively sharp and well-defined posterior keel on the oral surface along the midline and two less sharply defined keels in the two postero-lateral interambulacra (Pl. 24, figs 5, 8).

The apical disc lies 37–46% of test length from the anterior border (mean = 43%, SD = 2·5%, N = 23). It is monocyclic, with four gonopores that open at around 10–13 mm test length. The gonopores are oval and there is no sign of any suture separating them from the central area of madrepores (Fig. 65C). Ocular plates are small and subtriangular in outline.

Petals are bowed and converge distally, though remaining open (Fig. 65A). The anterior petal is the longest and the least bowed. It has about 20 pore-pairs in a column at test length of 10 mm, rising to 39 at 21 mm test length. The perradial portion of the ambulacrum is about 1·5 times the width of a single pore zone. Lateral and posterior petals are 60–86% of the anterior petal in length and are more strongly bowed. In all petals the two columns are of equal length. The posterior petals end well short of the periproct.

All pores below the petals are single. The phyllodes are well developed and strongly bowed but are only slightly sunken (Pl. 24, figs 1, 5, 12). The first ambulacral plates are elongate and bootshaped in outline, with small buccal pores (Fig. 65D). There is an outer series of closely packed pores and a shorter inner series of equally closely spaced pores (Pl. 24, fig. 12; Fig. 65D). There are 10 or 11 pores in the outer series of lateral and posterior phyllodes, and 9 or 10 in ambulacrum III. There are 4 or 5 pores in the inner series in all ambulacra. Despite the large number of individuals available, none show the detailed plating of the phyllode region adequately. The outer series of pores lie on a series of narrow plates that do not reach the perradius. Internally there is a second series of plates housing the inner series of pores. These may be oblique, but in no specimen is the plating in this region clear.

The peristome is pentagonal, slightly broader than long in larger individuals, and situated 33–39% test length from the anterior border (mean = 36%, SD = 1·5%, N = 23). The peristome width is 7–12% of test length and its length is 85–100% of its width. The peristome is sunken with well developed vertical walls. The surrounding interambulacral areas are developed into short, projecting, knob-like bourrelets, which do not, however, impinge on the peristome (Pl. 24, fig. 12).
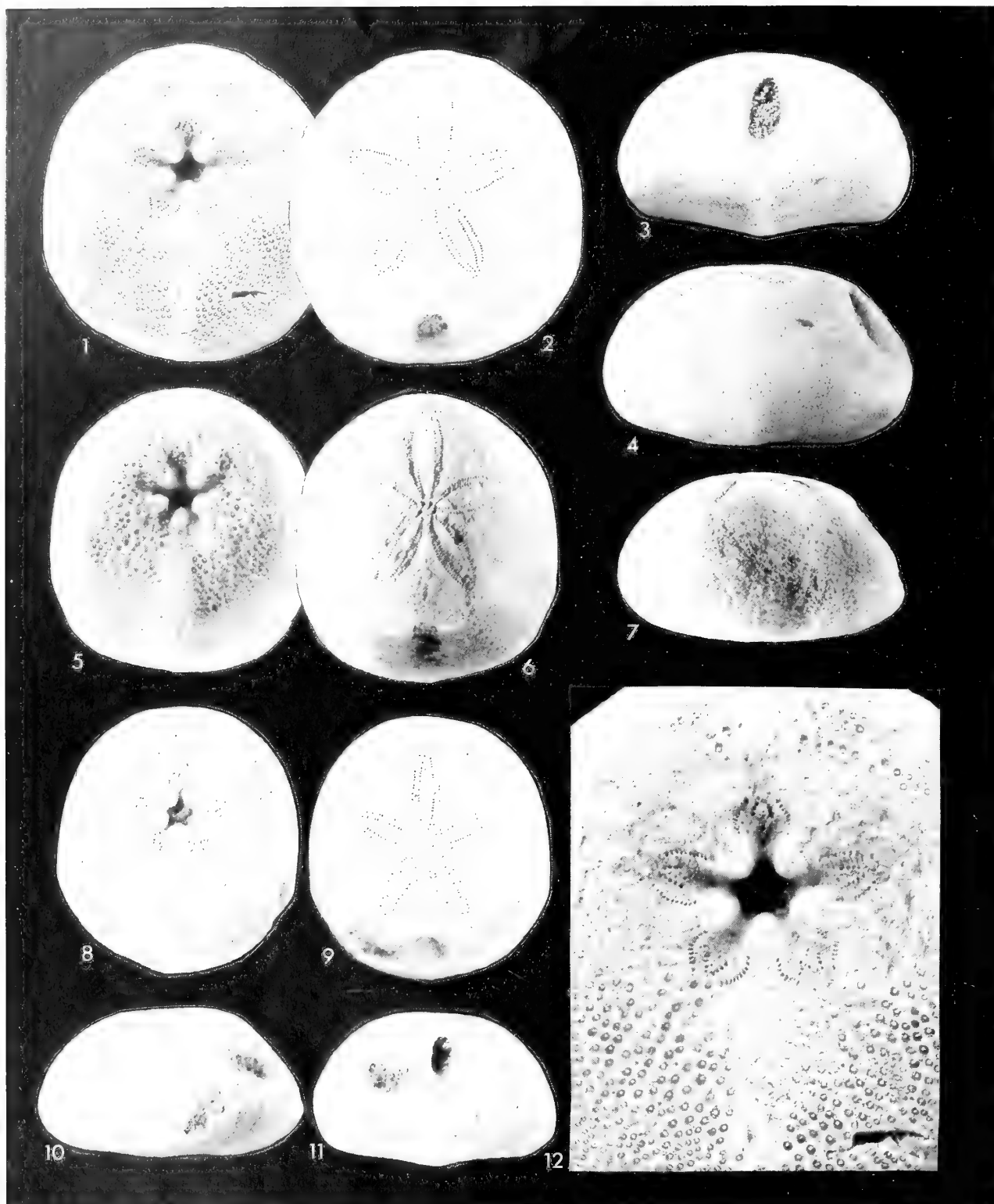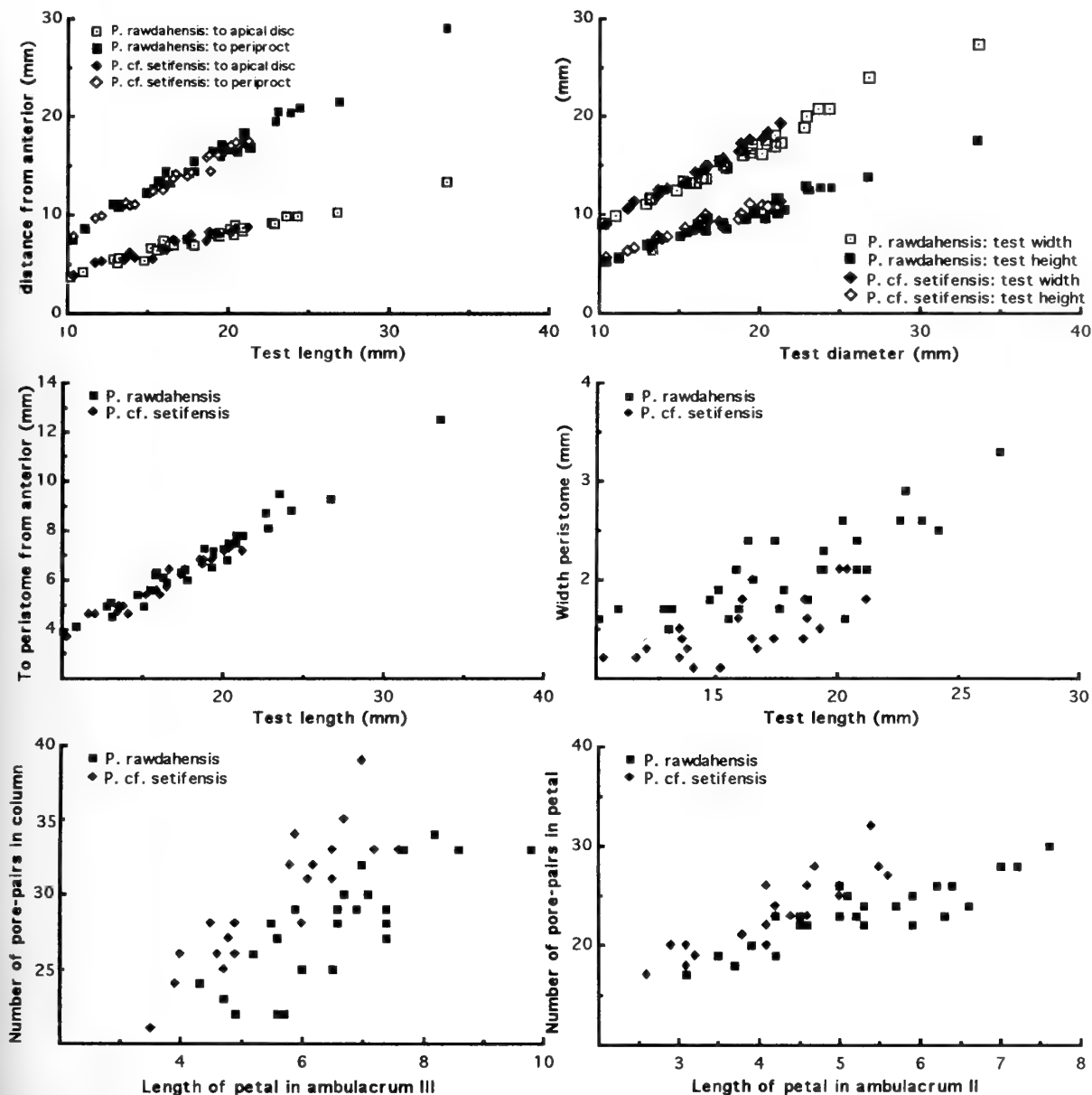
Fig. 64 Biometric data for *Petalobrissus rawdahensis* sp. nov. and *P.* cf. *setifensis* (Cotteau).

The periproct is clearly visible from above and opens 77–87% test length from the anterior border (mean = 82%, SD = 2·7%, N = 23). It is longitudinal, with a width that is 41–65% of its height. The opening is near vertical, with slightly invaginated walls forming a short, parallel-sided anal sulcus. There is a subanal rostrum (Pl. 24, figs 2, 6, 9–11).

Tuberculation is fine and uniform aborally, slightly coarser adorally. On the oral surface there is a narrow band free of tubercles down the midline of the posterior interambulacrum. This is finely granular and tapers towards the posterior.

REMARKS. This species is problematic to place on account of its monobasal apical disc. In general shape and plating it conforms closely to species of *Petalobrissus*, having very similar phyllodes and bourrelets, a similar longitudinal periproct set far back on the test, and only a remnant anal

sulcus. However, the type species of *Petalobrissus* has a tetrabasal apical disc according to Kier (1962), whereas *P. rawdahensis* has a monobasal disc. *P. rawdahensis* also bears a strong resemblance to small *Hardouinia* species, especially in the characteristic keeled oral surface, bowed petals and well developed bourrelets. However, in the type species of *Hardouinia*, *H. mortonis*, the phyllodes are more strongly arcuate with the inner series arranged distally as an integral part of the arc. Furthermore, the peristome opens subcentrally. In the type species of *Procassidulus*, *P. lapiscancri* (Goldfuss) from the Maastrichtian of Maastricht, the phyllodes are less arcuate and the inner series is parallel to the outer series of pores. *P. rawdahensis* also differs from *P. lapiscancri* (Goldfuss) in being larger, more rounded in profile and oval in outline, and in having more pores in its
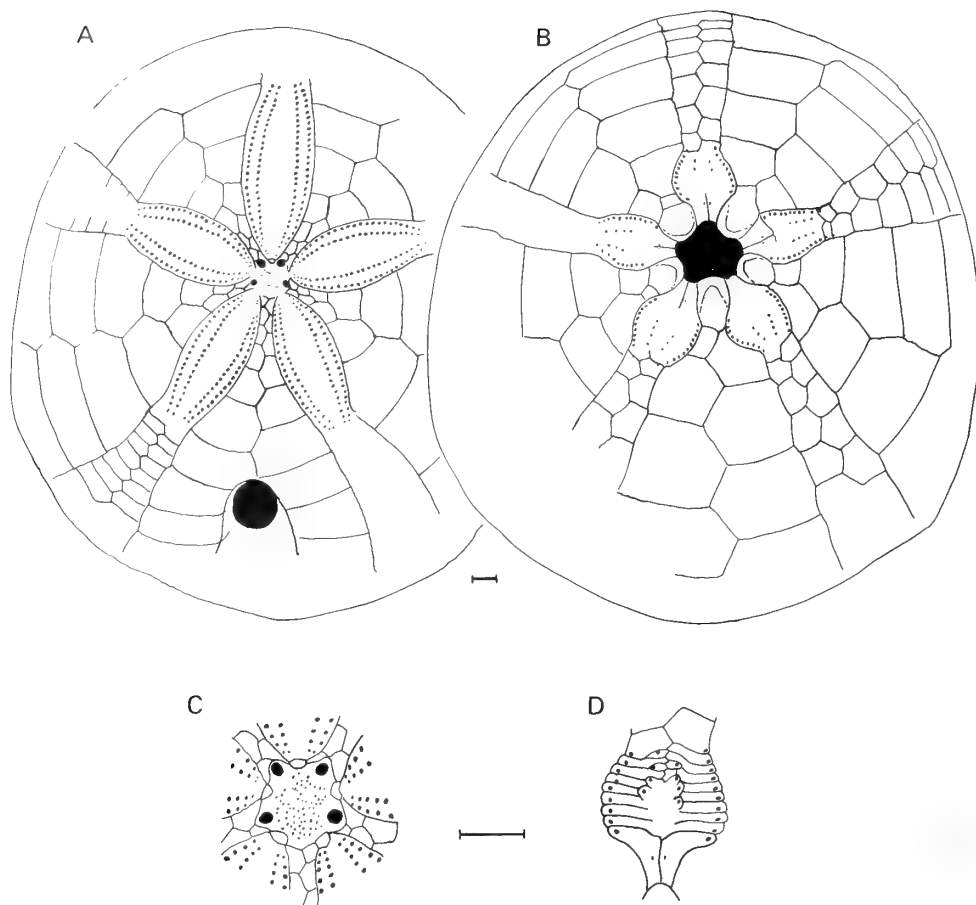
Fig. 65 Camera lucida drawings of plating in *Petalobrissus rawdahensis* sp. nov. **A**, apical surface, BMNH EE3485; **B**, oral surface, BMNH EE3487; **C**, apical disc, BMNH EE3476; **D**, One phyllode, peristome margin at base, BMNH EE3484. Scale bars = 1 mm.

phyllodes at comparable sizes. Pending revision of this group, *P. rawdahensis* is placed in the genus *Petalobrissus*.

Petalobrissus rawdahensis is easily distinguished from *Petalobrissus* cf. *setifensis* (Peron & Gauthier), which occurs in the same section, by its more angular outline, its posterior keel and slope on the oral surface, its smaller, less quinquelobate peristome and its more bowed and densely pored petals.

Petalobrissus cf. *setifensis* (Cotteau, 1866)   Pl. 25, figs 1–10; Figs 64, 66

cf. 1866   *Echinobrissus setifensis* Cotteau: 267, pl. 14, figs 13–15.
cf. 1962   *Petalobrissus setifensis* (Cotteau); Kier: 125, pl. 16, figs 10–13.
     1989   *Petalobrissus inflatus* Gauthier & Thomas; Ali: 405, fig. 5 (9).

MATERIAL STUDIED. Thirty one specimens were used for the biometric analysis: BMNH EE3505–10, EE3512–28, EE3530, EE3532, EE3535, EE3537–41. An additional 269 specimens were collected.

OCCURRENCE. Apart from five specimens collected from the scree at Jebel Buhays, section 1, and a single specimen from bed 9 at Jebel Bu Milh, all the material comes from sections at Jebel Rawdah. The distribution of specimens is as follows:
Jebel Rawdah, section 1: bed 3 (18).
Jebel Rawdah, section 2: bed 8 (9); bed 11 (124); beds 12/13 (4); bed 14 (15); bed 19 (23); bed 21 (44); bed 26 (3).
Jebel Rawdah, section 3b: bed 2 (4).
Jebel Rawdah, section 4: bed 4 (1); beds 8/9 (3).

DESCRIPTION. Tests are oval in outline, uniformly rounded at the anterior and slightly flattened at the posterior (Pl. 25, figs 1, 2). Test length ranges from 10 to 33 mm. Test width is 82–93% of test length (mean = 87%, SD = 2·9%, N = 31), with the widest point slightly posterior of midlength. Test height is 49–61% of test length (mean = 54%, SD = 3·1%, N = 31), with the highest point at or a little posterior of the apical disc. In profile the anterior is uniformly rounded, the posterior obliquely truncated (Pl. 25, figs 4, 10). The ambitus is rounded and about one-quarter of the test height above the base. The oral surface is flat, with a very slight depression towards the peristome.

The apical disc lies 37–48% test length from the anterior border (mean = 42%, SD = 2·4%, N = 31) being relatively more anterior in larger individuals (Fig. 64). It is monocyclic with no evidence of any sutures between the gonopores and central madreporite region in any specimen, even where ocular plate sutures are clear (Fig. 66D). However, the
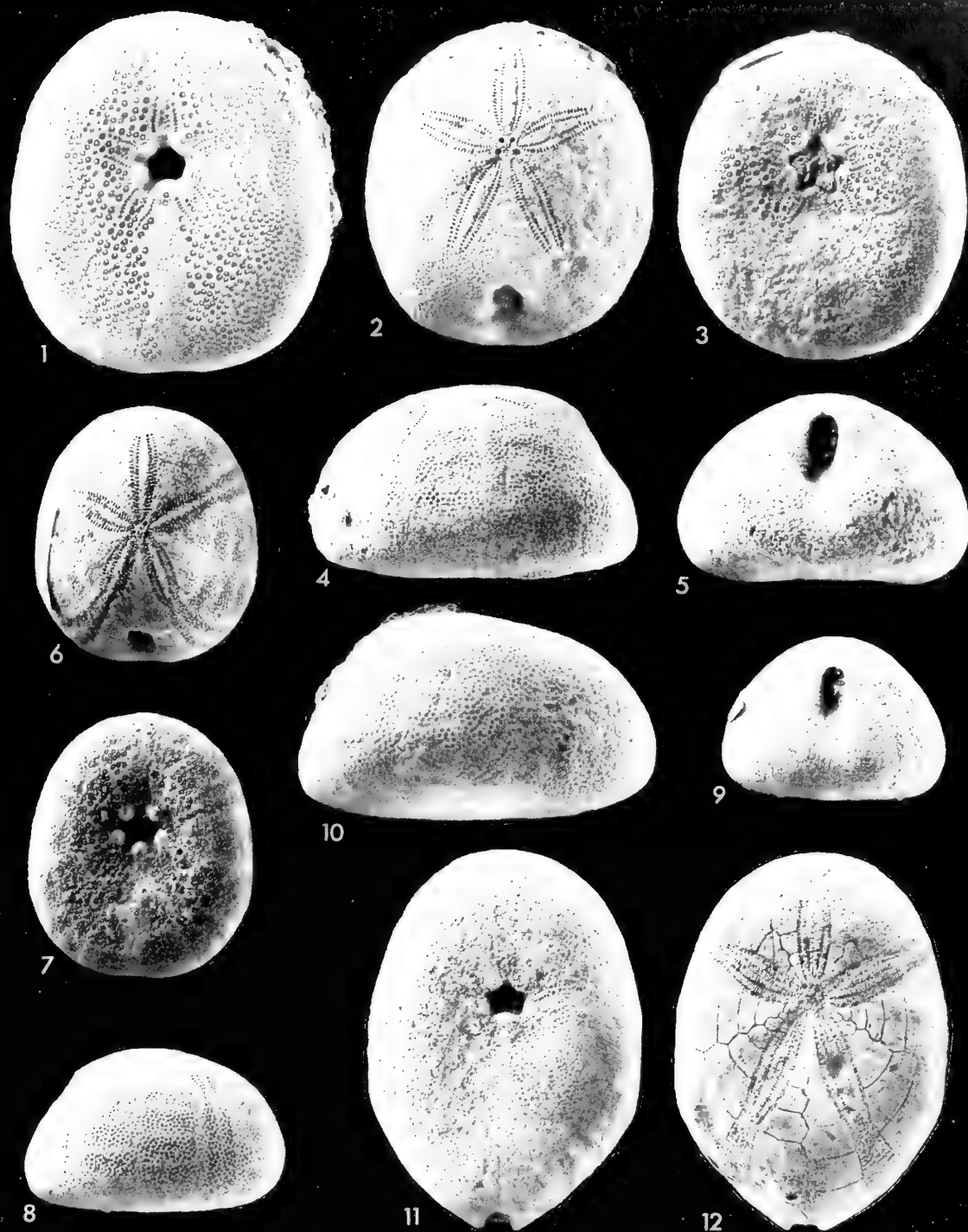
PLATE 25

Figs 1–10 *Petalobrissus* cf. *setifensis* (Cotteau). **1, 10,** BMNH EE4341; **1**, oral; **10**, lateral; both × 3 Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation. **2–5,** BMNH EE3519; **2**, apical; **3**, oral; **4**, lateral; **5**, posterior; all × 3. Jebel Rawdah, section 2, bed 11. **6–9,** BMNH EE3536; **6**, apical; **7**, oral; **8**, lateral; **9**, posterior; all × 3. Jebel Rawdah, section 2, bed 19.

Figs 11, 12 *Arnaudaster cylindriformis* sp. nov. BMNH EE4324, depressed variety; **11**, oral; **12**, apical; both × 2 (see also Pl. 29, Figs 6, 9). Jebel Rawdah, section 2, in scree at level of bed 14.
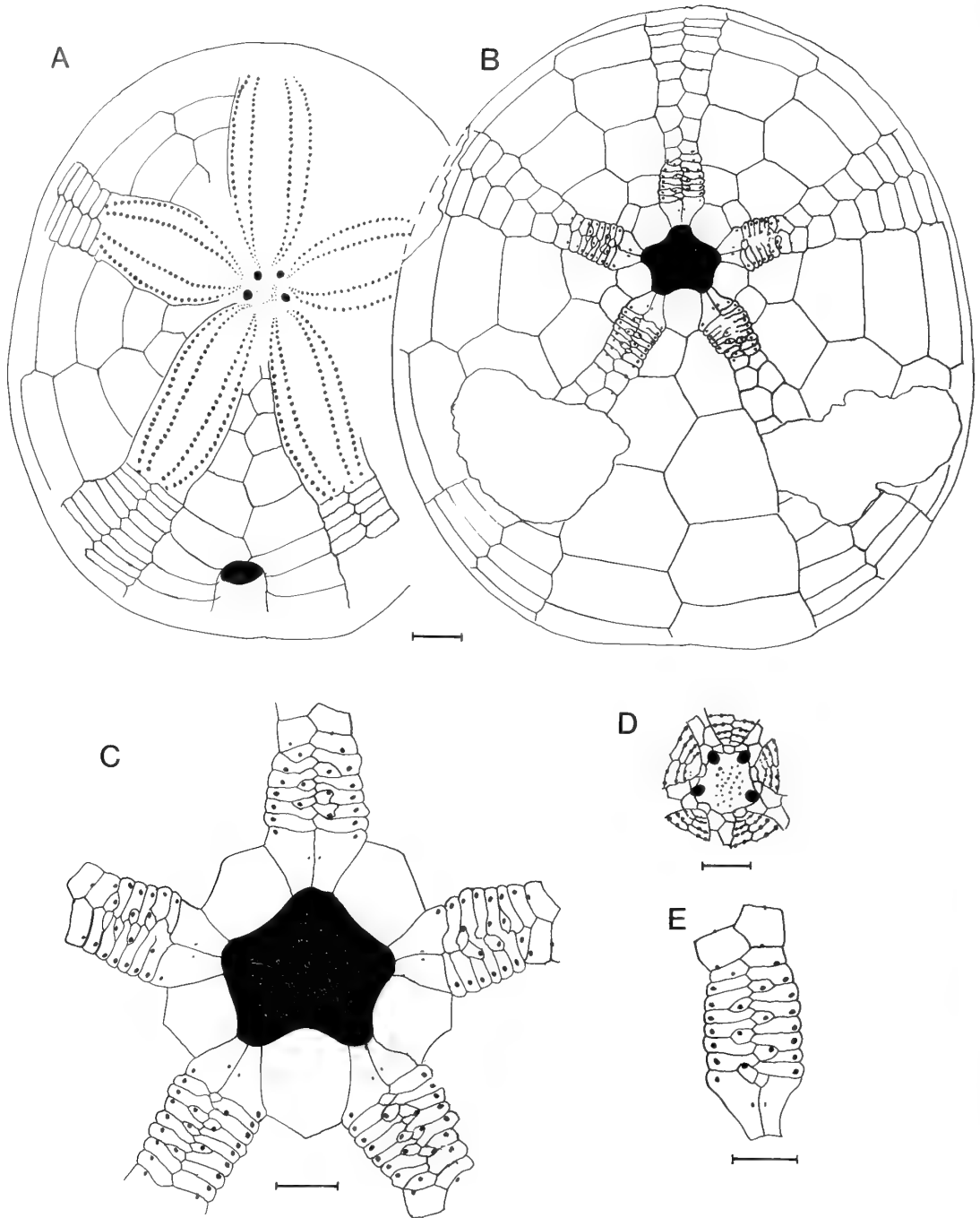
Fig. 66 Camera lucida drawings of plating in *Petalobrissus* cf. *setifensis* (Cotteau). **A,** apical surface, BMNH EE3514; **B,** oral surface, BMNH EE3535; **C,** phyllode plating, BMNH EE3524; **D,** apical disc, BMNH EE3524; **E,** single phyllode, peristome margin to base, BMNH EE3535. Scale bars: A, B = 2 mm, C-E = 1 mm.

madrepores do not usually extend up to the gonopores. Gonopore diameter varies markedly between individuals of the same test length, indicating sexual dimorphism in this species. Gonopores appear at around 10–12 mm test length.

Petals are lanceolate, with almost straight lines of inner pores and only slightly bowed lines of outer pores in all petals (Pl. 25, fig. 2; Fig. 66A). All are distally open and both inner

and outer pores are subcircular in outline. The anterior petal is the longest and has about 22 pore-pairs in a column at 15 mm test length, rising to 39 at 33 mm test length. Petals in ambulacra II and IV are 65–93% of the length of the anterior petal (mean = 80%, SD = 6·6%, N = 28), whereas the posterior petals are 73–100% of the length of the anterior petal (mean = 87%, SD = 6·6%, N = 28). The posterior

petals end well short of the periproct.

All pores below the petals are single. The phyllodes are only slightly expanded and are flush with the surrounding test (Pl. 25, figs 1, 3). Irrespective of size there are 7 or 8 pores forming an outer series and 3 or 4 pores forming an inner series in the phyllodes (Figs 66C, E). The first ambulacral plates are boot-shaped and carry small buccal pores, but are not particularly elongate. The inner series of pores are found on small occluded plates which are separated from one another (i.e. they do not form a continuous inner series of plates). Each is separated from its neighbours by two of the outer plates. Sphaeridial pits are confined to the area between the most adoral of the inner series of pores and the buccal pores. There are just two or three in each column.

The peristome is quinquelobate, and relatively large (Fig. 66C). Its length is 9–16% of the test length (mean = 11%, SD = 1·6%, N = 29) and 81–120% of its width. There is a distinct vertical-walled well to the peristome, covered in fine miliary tubercules. Bourrelets are not developed. However, the interambulacral margins to the peristomial well are elevated slightly, forming a lip-like rim (Pl. 25, fig. 1).

The periproct is longitudinal and clearly visible from above (Pl. 25, figs 2, 6). It lies 76–92% of test length from the anterior border (mean = 85%, SD = 3·5%, N = 31). It is about twice as tall as wide (mean width = 48% of height). There is a short parallel-sided anal sulcus that stops short of the ambitus.

All tubercles are sunken, those adorally being noticeably larger than the aboral ones. There is a median naked zone on the oral surface in both the anterior ambulacrum and the posterior interambulacrum (Pl. 25, figs 1, 3, 7). The anterior zone is short and does not reach the ambitus, but the posterior zone is broader, approximately parallel-sided and reaches the posterior border. It is finely granular.

REMARKS. This species could at first glance be confused with *Petalobrissus rawdahensis*, but is distinguished on several counts. It has a larger, more quinquelobate peristome, a flatter base without the posterior keel, it lacks bourrelets and has less inflated phyllodes with fewer pores. It has more parallel-sided petals with less densely packed pore-pairs. It resembles certain other species of *Petalobrissus* in its overall shape and form, but is distinguished by its monobasal apical disc. In particular it most closely resembles *P. cubensis* (Weisbord), particularly in its floscelle structure. However, it differs from *P. cubensis* in having a narrower posterior naked zone on its oral surface, in having its apical disc less anterior and in having a proportionally longer anterior petal.

It also comes close to certain species currently assigned to *Rhynchopygus* in test shape and floscelle structure, but differs in having a longitudinal rather than a transverse peristome. It is closest to *P. setifensis* (Peron & Gauthier), from the Maastrichtian of Algeria, but differs in some minor details, having a flatter base and more quadrate outline with less rounded ambitus, and in having fewer inner-series pores.

This species was identified by Ali (1989) as *Petalobrissus inflatus* (Gauthier & Thomas), but *P. inflatus* is a Cenomanian species that differs in several respects, notably in having much longer and more densely pored petals at equivalent sizes. These petals are strongly bowed in *P. inflatus* and the posterior pair extend back to a point level with the opening of the periproct.

Cassidulus oldhamianus Stolizcka, from the Maastrichtian Arrialoor Group of Southern India may be comparable, and appears similar in overall form. However, that species is inadequately described and figured and no examples of it are available for comparison. At present it is impossible to say what genus the species belongs to.

Petalobrissus linguiformis (Peron & Gauthier, *in* Cotteau, Peron & Gauthier, 1881) Pl. 23, figs 5, 6; Pl. 26, figs 1–6; Figs 67, 68

TYPES. Syntypes are the two measured specimens in the Peron & Gauthier collections referred to in Cotteau *et al.* (1881: 162).

MATERIAL STUDIED. Ten specimens, BMNH EE3334–35, EE3337, EE3341–45, EE4319, EE5021, were measured for the biometric analysis. An additional 11 specimens were also collected.

OCCURRENCE. This species was originally described from the Maastrichtian of Algeria, and has since been reported from Tunisia and Egypt. Apart from one specimen collected loose at Jebel Buhays, section 3, all specimens come from Jebel Rawdah. It is found at the following localities and horizons:
Jebel Buhays, section 1: loose in the scree, derived from the lowest few metres of the Simsima Formation (1).
Jebel Rawdah, section 2: bed 14 (4); bed 19 (5); bed 20 (1); bed 21 (4); loose from upper part of section (beds 14–21) (5).
Jebel Rawdah, section 4: loose in scree (1).

DIAGNOSIS. An elongate *Petalobrissus* with a narrow, almost vertical periproct and short anal sulcus set very far towards the posterior on the upper surface. Phyllodes are very strongly developed, with prominent bourrelets and outer and inner series of pores forming well-defined lines. There are up to 20 pores in the outer series and 10 in the inner series. In addition there are well developed rows of sphaeridial pits down the perradius.

DESCRIPTION. Tests are ovoid in outline, uniformly rounded at the anterior and slightly more pointed towards the posterior, with a slight, but distinct, anal cleft (Pl. 26, figs 1, 2). Tests range in size from 13 to 50 mm in length. The widest point on the test lies about two-thirds the distance from the anterior border. Test width is 76–87% of test length (mean = 82%, SD = 4·6%, N = 10). In profile the test is depressed, with a height that is 43–48% of test length (mean = 46%, SD = 1·8%, N = 9). The upper surface is slightly domed with the tallest point slightly posterior to the apical disc. The ambitus is uniformly rounded and lies at about one-third test height. The posterior is more or less truncated (Pl. 23, fig. 6).

The apical disc lies 34–44% test length from the anterior border (mean = 40%, SD = 3·0%, N = 7). It is tetrabasal, with a large madreporite plate and three small genital plates projecting into the interambulacra (Fig. 68D). These genital plates are U-shaped because of the gonopore that opens along their outer margin. Genital plates lie separated from adjacent ocular plates.

Petals are well developed (Pl. 26, fig. 5: Fig. 68B). The anterior and posterior pair of petals are both rather straight and remain open distally, whereas the antero-lateral pair of petals are more bowed and converge distally (Pl. 23, fig. 5). The perradial zone is about twice the width of a pore zone. The anterior petal is noticeably longer than other petals and extends more than three-quarters of the distance to the ambitus. Petals II and IV are 61–74% of the length of the
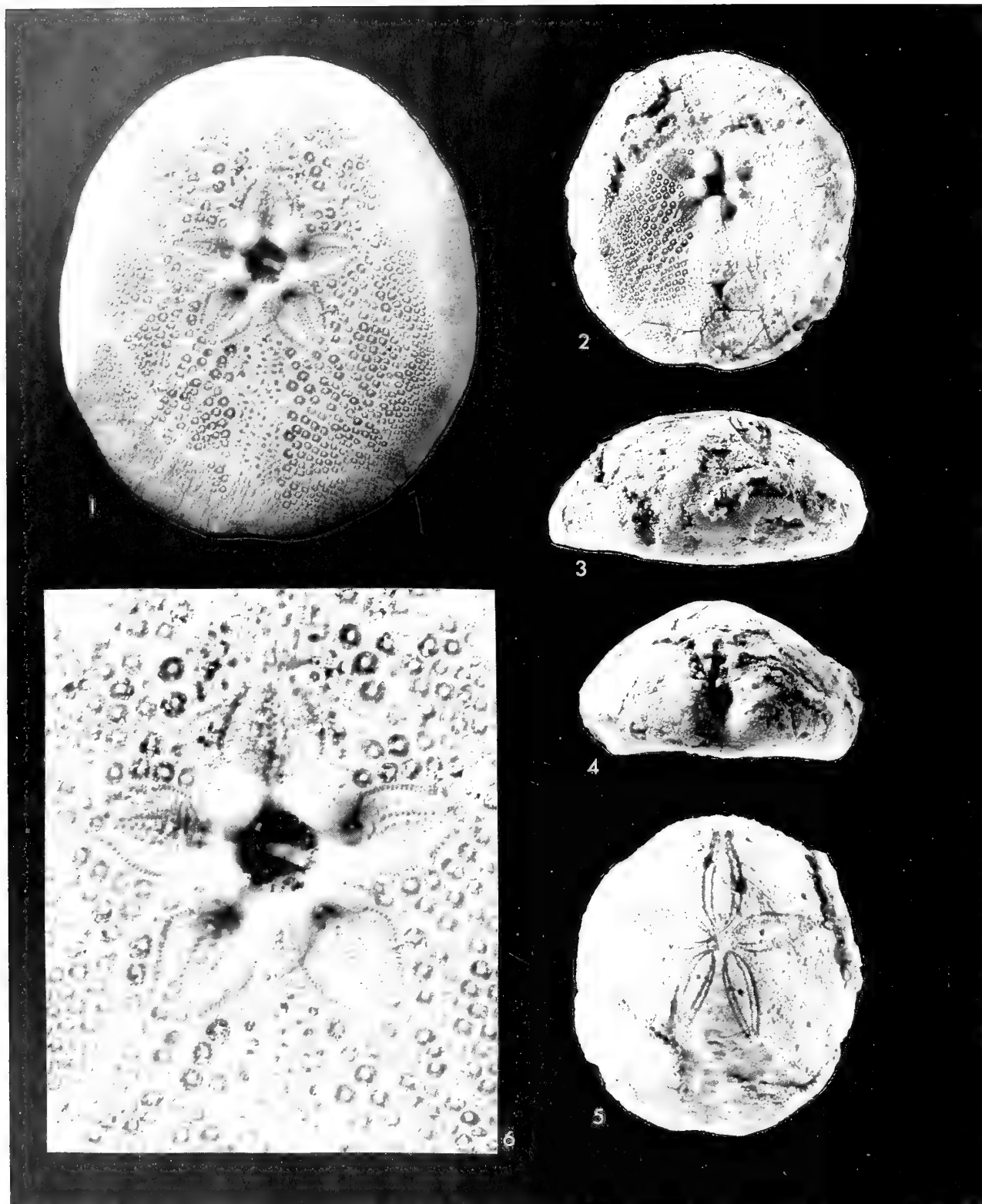
Figs 1–6 *Petalobrissus linguiformis* (Peron & Gauthier). **1, 6,** BMNH EE4319; **1,** oral, × 3; **6,** detail of peristome, × 6. Jebel Rawdah, section 2, beds 19/20. **2–5,** BMNH EE3345; **2,** oral; **3,** lateral; **4,** posterior; **5,** apical; all × 2. Jebel Rawdah, section 2, loose, derived from beds 14–21.
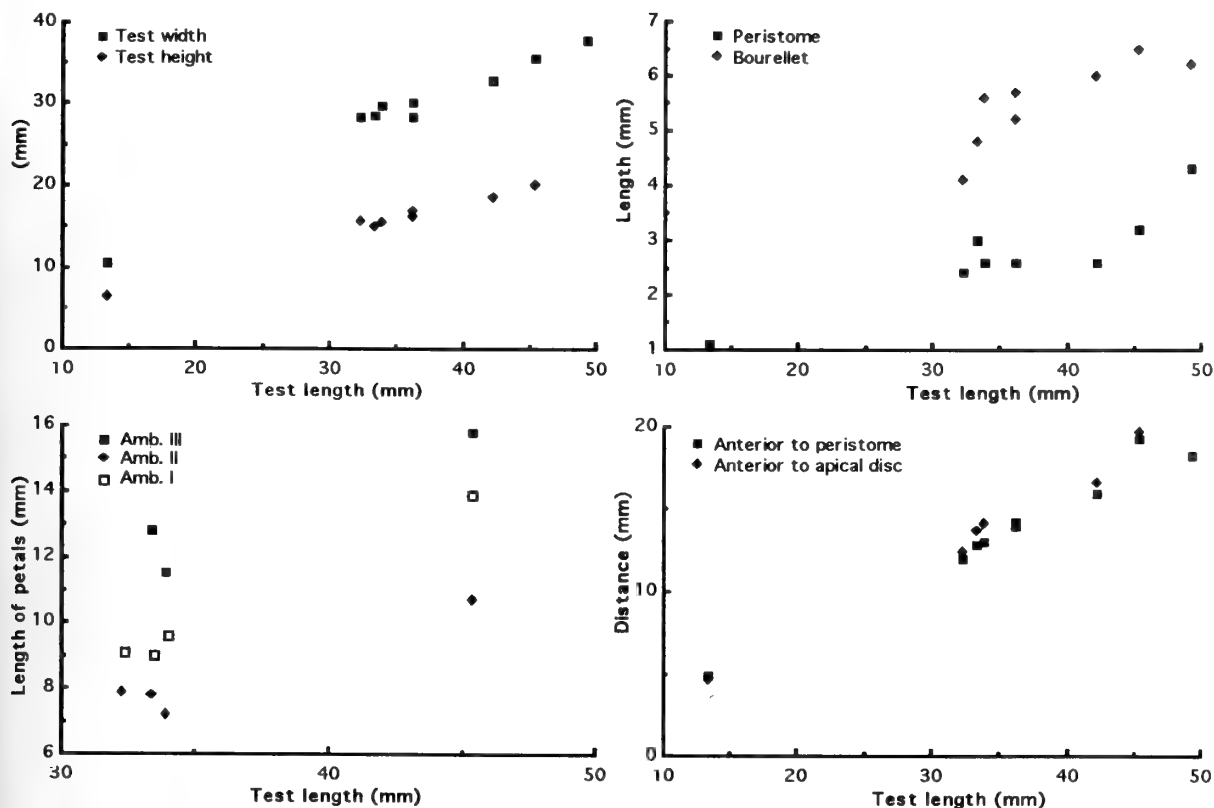
Fig. 67 Biometric data for *Petalobrissus linguiformis* (Peron & Gauthier).

anterior petal, wheras petals I and V are 71–89% of the length of the anterior petal. The posterior petal extends less than two-thirds the distance from the apical disc to the periproct.

All pores below the petals are single. The phyllodes are well developed and bow outwards strongly towards the peristome. They become slightly sunken towards the peristome, with the buccal pores situated in a shallow depression separated from the peristomial well (Pl. 26, fig. 6). There are two series of pores, well separated from each other and with pores closely packed together in each row. The outer row comprises some 17 to 20 pores, the inner series 7 to 9 (Fig. 68C). The first ambulacral plates are squat and broad, with buccal pores situated near their adambital edge and well separated from the peristome. Pores in the outer series are bowed and every third plate is smaller and does not reach the inner series of plates. These pores may be slightly offset, marking the incipient development of a median series of pores. The inner series of pores are situated towards the outer edge of a double column of occluded plates. Each plate carries a sphaeridial pit on its perradial side, there being some 8–10 sphaeridial pits forming a well defined column on either side of the perradial suture.

The peristome is subcircular to pentagonal and is approximately as broad as it is wide. It is 69% of test length in diameter and lies 37–42% of test length from the anterior border. There are short, pointed bourrelets which project outwards but do not impinge on the peristome (Pl. 26, fig. 6).

The periproct lies close to the posterior border, and is clearly visible from above (Pl. 26, fig. 5). It is longitudinal,

being 27–40% as wide as it is tall (Pl. 26, fig. 4). It is slightly V-shaped, narrowing adapically, and opens into a short anal sulcus with parallel-sided walls. The periproct is almost vertical in orientation.

Tubercles are minute and densely packed aborally, but coarser and less dense adorally. There is a relatively broad naked zone in the posterior interambulacrum that runs from the peristome to the posterior border. This is 13–18% of the test width in width. It is covered in a reticulate pattern of pits.

REMARKS. This species is readily differentiated from other cassiduloids described here by its highly developed phyllodes, its almost posterior periproct and its characteristic shape. The only species that come close are the southern Indian *P. testudo* (Forbes) and *P. emys* (Stoliczka), both from the Maastrichtian. Both have a similar test shape, with the posterior slit-like periproct, the anal notch and the projecting bourrelets. *P. testudo* has much less developed phyllodes with few pores in the inner series and only 8–10 pores in its outer series. *P. emys* is too poorly known to be compared closely as the original figures and description omit many important details such as phyllode structure. It may eventually prove to be synonymous with *P. testudo*.
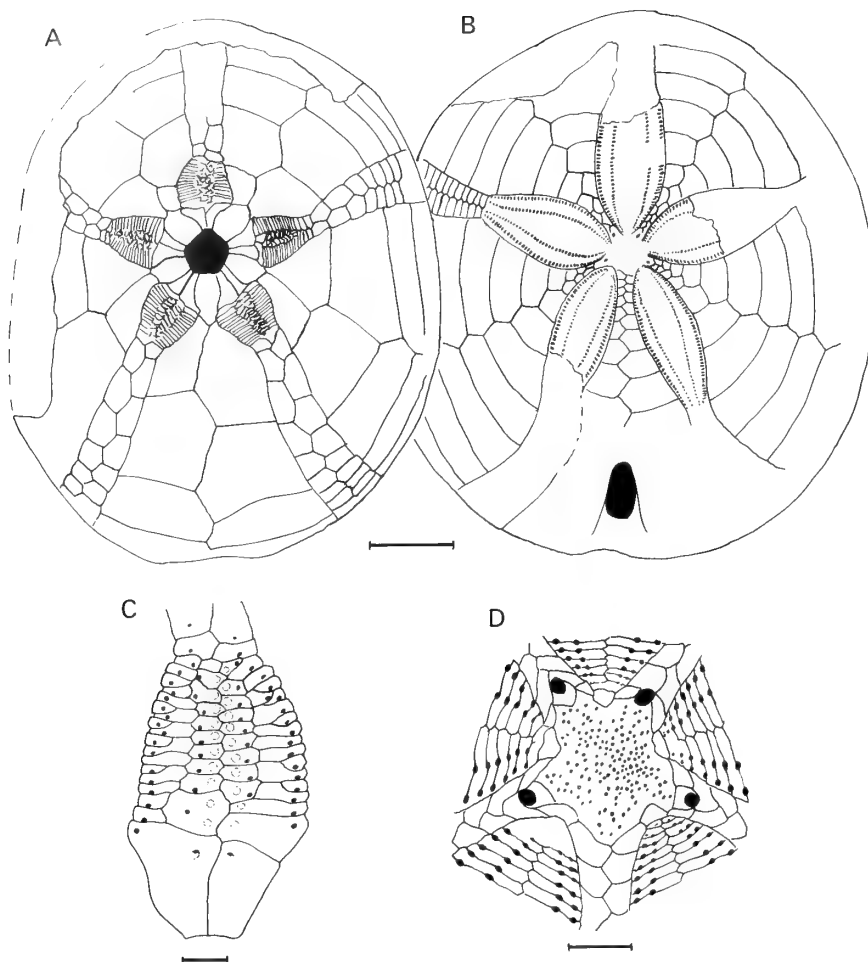
Fig. 68   Camera lucida drawings of plating in *Petalobrissus linguiformis* (Peron & Gauthier). **A,** oral surface, BMNH EE3344; **B,** apical surface, BMNH EE3345; **C,** oral phyllode, peristomial margin at base, BMNH EE3334; **D,** apical disc, BMNH EE3345. Scale bars: A, B = 5 mm; C, D = 1 mm.

Genus *STIGMATOPYGUS* d'Orbigny, 1856

Stigmatopygus pulchellus? sp. nov. Pl. 27, figs 1–8; Figs 69, 70

TYPES. Holotype BMNH EE4314, paratypes, BMNH EE3324–25, EE3329–30, EE3332–33, EE4312–13: all nine specimens were used for the biometric analysis given below in the description.

OTHER MATERIAL. In addition a further six specimens were collected.

OCCURRENCE. The species has been found only at Jebel Rawdah, section 2, at the following horizons: bed 14 (6); bed 19 (1); bed 21 (7); loose in scree, derived from beds 14–21 (1).

DESCRIPTION. Tests are elongate oval in outline, with a rounded anterior and a small posterior indentation (Pl. 28, figs 2–7). Tests range in length from 37 to 68 mm. Test width is 77–84% of test length (mean = 80%, SD = 1·9%, N = 9) and the widest point is slightly posterior of midlength. Test height is 41–56% of test length (mean = 47, SD = 4·9%, N = 9). The test has a depressed profile with the highest point

coincidental with the apical disc and thus anterior of centre. There is a posterior notch marking the position of the periproct, and a small heel underneath the periproct in profile (Pl. 27, fig. 5).

The apical disc lies anterior of centre, some 32–40% of test length from the anterior border (mean = 37%, SD = 3·4%, N = 7). It appears to be tetrabasal, although the madrepores extend almost up to the start of the gonopores (Fig. 70D). There is no evidence for sexual dimorphism amongst the specimens to hand.

The petals are bowed, and are widest about one third of their distance from the apex (Pl. 27, fig. 7). The anterior petal has columns of equal length and the inner series of pores are almost straight. It is 22–27% of test length in length. The interporal zone is about twice as wide as the pore zone. Petal III is significantly longer than the rest. The petals in ambulacra II and IV are bowed and converge distally but remain open. The pore columns in the posterior petals are significantly different in length, with the inner series some 8–10 pore-pairs shorter than the outer column in larger specimens. These petals are also the narrowest.

All pores below the petals are single. Towards the peristome phyllodes are well-developed, and expand as an open
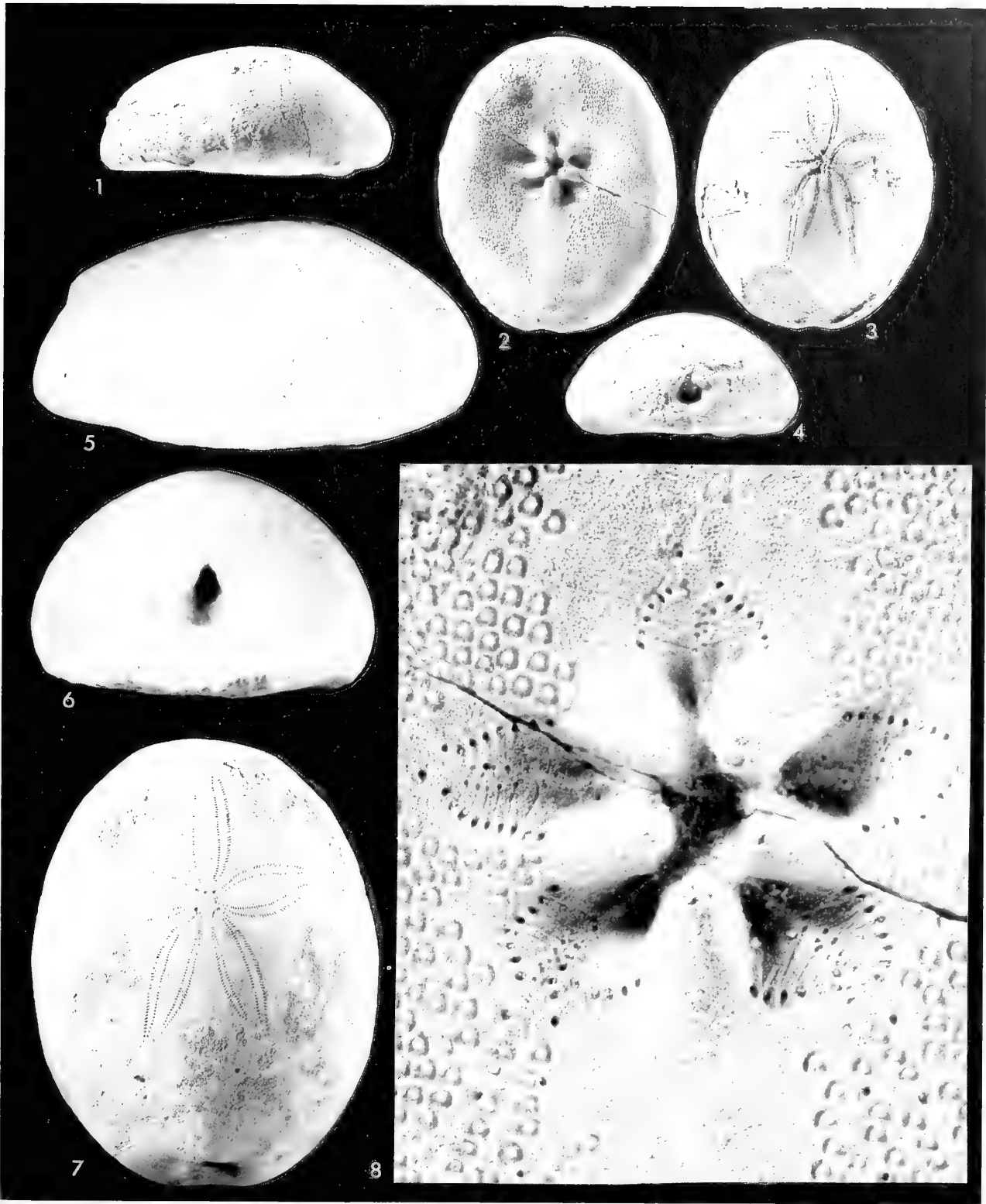
PLATE 27

Figs 1–8 *Stigmatopygus? pulchellus* sp. nov. **1–4, 8,** BMNH EE4314, holotype; **1**, lateral, × 1; **2**, oral, × 1; **3**, apical, × 1; **4**, posterior, × 1; **8**, detail of peristomial region, × 5. Jebel Rawdah, section 2, bed 19. **5–7,** BMNH EE4313, paratype; **5**, lateral; **6**, posterior; **7**, apical; all × 2. Jebel Rawdah, section 2, bed 14.
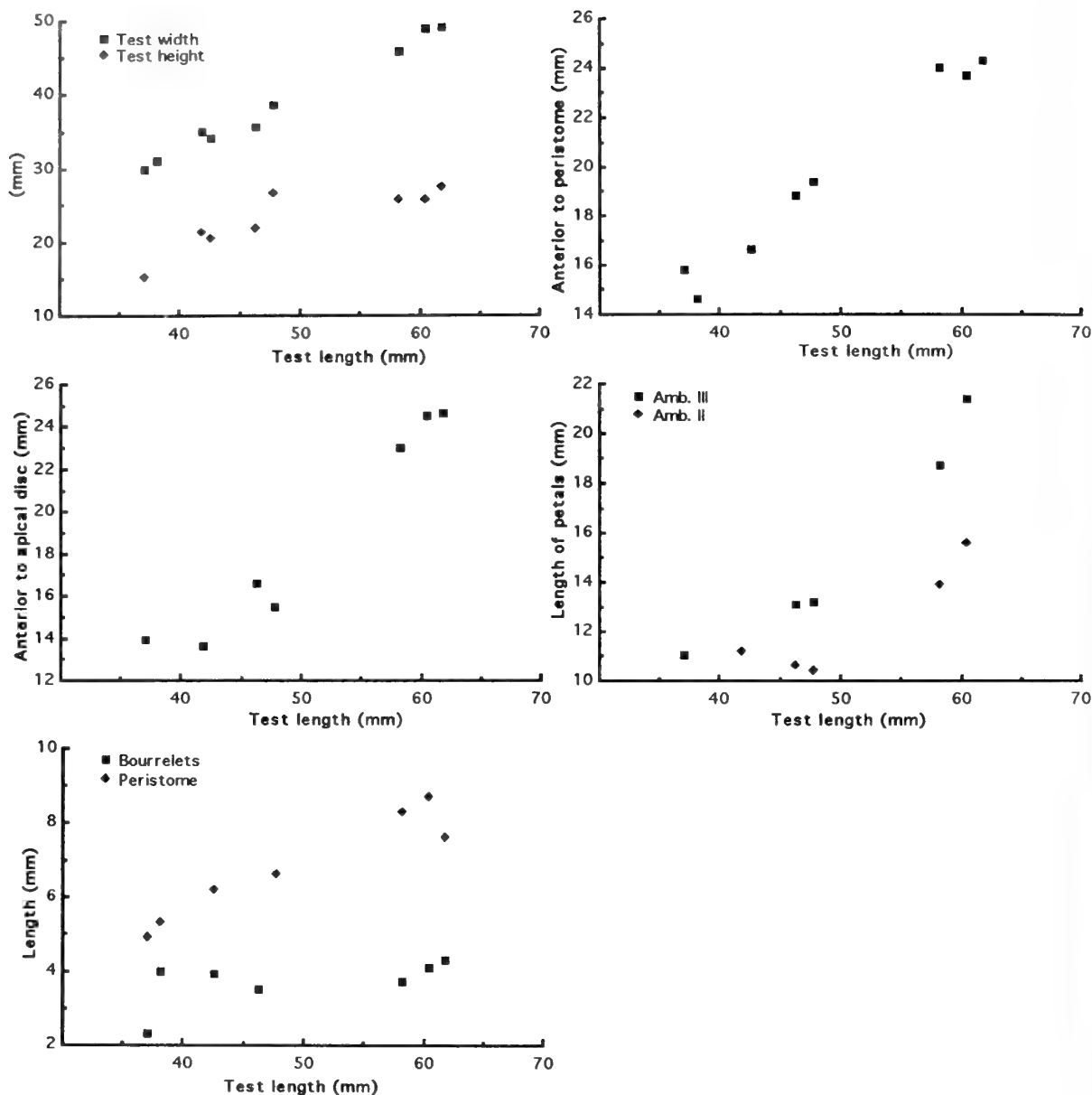
Fig. 69 Biometric data for *Stigmatopygus pulchellus* sp. nov.

'V' (Pl. 27, fig. 8). There are five or six pores in each series along the margin with an additional one, or rarely two inner pores at the distal end of the phyllodes (Fig. 70C). Usually there is only one occluded plate in each phyllode, all other plates extending from the adradial to the perradial suture. The first ambulacral plates are long and boot-shaped, with buccal pores that are much smaller than those composing the remainder of the phyllodes (Fig. 70C). Sphaeridial pits occur on each plate close to the midline, forming an alternating series, 4 or 5 per column. The phyllodes lie sunken relative to the surrounding test with buccal pores on the adoral walls of this depression, rather than in the peristomial well.

The peristome is pentagonal and either equilateral or slightly longer than wide (Pl. 27, fig. 8). Bourrelets are well developed, being straight-sided to weakly wedge-shaped in

outline and projecting upwards strongly. They do not, however, project over the peristome.

The periproct is only just visible from above, being situated more or less posteriorly (Pl. 27, figs 6, 7). It is triangular in shape with an upper pinched portion and a broader, more rounded lower portion. It is typically slightly taller than broad. There is a subanal platform that extends as an invaginated floor to the periproct. There is a slight aboral lip to the periproct. It lies 21–34% above the base of the test (mean = 27%, SD = 5·5%, N = 7).

Tuberculation is fine and uniform aborally, slightly coarser orally. There is a very broad and well-developed naked zone running the length of the posterior interambulacrum. A smaller naked zone is also present anteriorly along the midline. These zones are covered in a very fine granulation
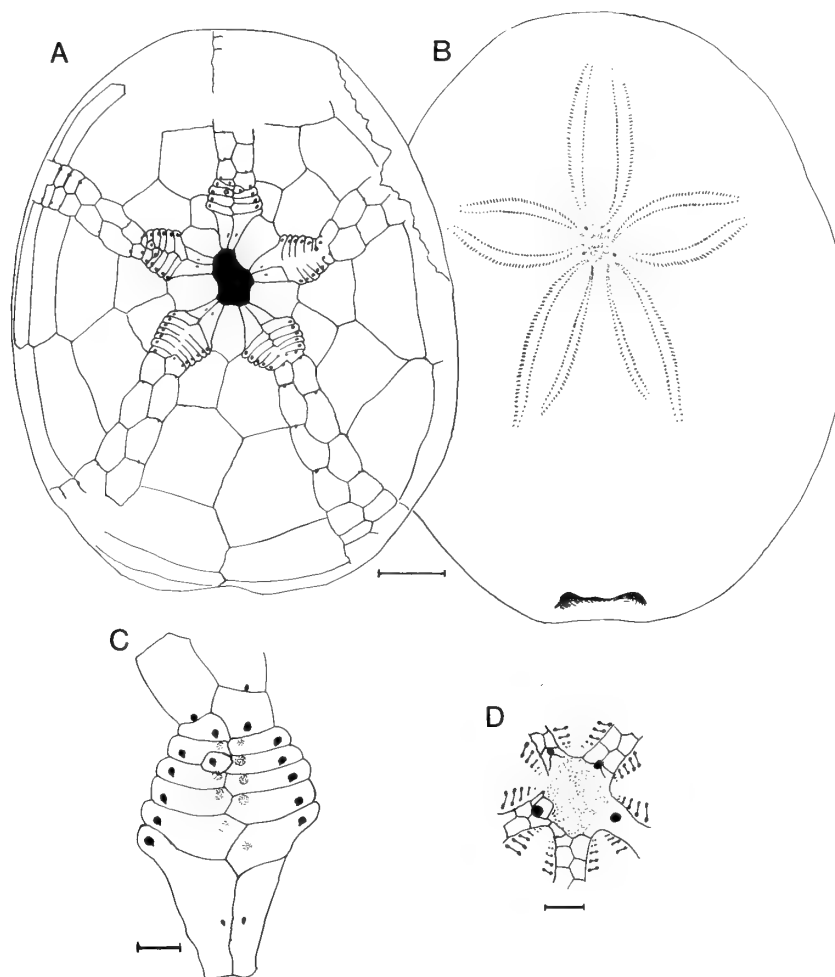
Fig. 70 Camera lucida drawings of plating in *Stigmatopygus pulchellus* sp. nov. **A,** oral surface, BMNH EE4312; **B,** apical surface, BMNH EE4314; **C,** phyllode plating, peristomial margin at base, BMNH EE4312; **D,** apical disc, BMNH EE3325. Scale bars: A, B = 5 mm; C, D = 1 mm.

but appear smooth to the naked eye.

REMARKS. This is a very distinct species, on account of its asymmetric posterior petals and keyhole-shaped periproct. Small forms resemble *Petalobrissus linguiformis* (Peron & Gauthier), but are easily distinguished from that species by their phyllode structure and periproct shape. *P. linguiformis* has a longitudinal periproct with a short parallel-sided anal sulcus, and also has much better developed phyllodes, with a separate series of inner occluded plates.

The new species undoubtedly comes closest to the type species of *Stigmatopygus*, *S. galeatus* d'Orbigny from the late Cretaceous of Angouleme, France. Both have a very similar test shape and periproct position and shape. Unfortunately, this species is very poorly known, the original description and figures being quite inadequate by today's standards. In particular its phyllode structure is unreported. Kier (1962) described the phyllode structure of another species *S. lamberti* Bessairie, from the Campanian of Madagascar, but this differs in being much wider and taller, with a much larger periproct. It also has better developed phyllodes, which are clearly bowed and comprise an outer series of some 12 pores

and an inner series of 4 or 5 pores. I am therefore not certain that *S. lamberti* is truly congeneric with the type species *S. galeatus*. Only re-study of the type (apparently lost), or topotype material will solve the problem. If the phyllode structure of *S. galeatus* is similar to that of *S. pulchellus*, then *S. lamberti* should be transferred to a new genus. On the other hand, if *S. galeatus* proves to have a phyllode structure similar to that of *S. lamberti*, then *S. pulchellus* should be made the type of a new genus. Consequently, *S. pulchellus* can only tentatively be placed in the genus *Stigmatopygus*.

S. galeatus can be distinguished from *S. pulchellus* by the fact that its petals are illustrated as being of equal length.
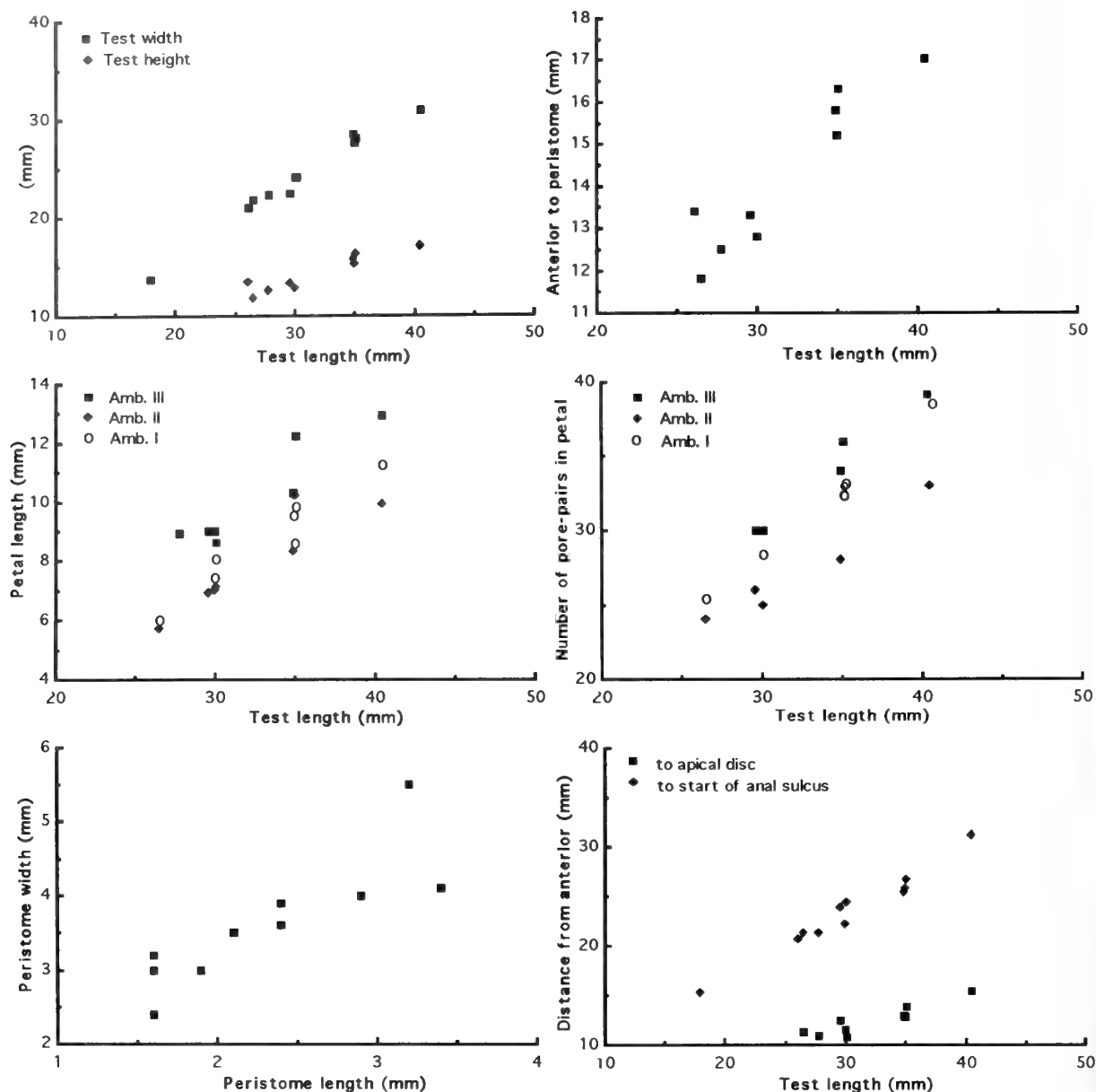
Fig. 71 Biometric data for *Nucleopygus magnus* sp. nov.

Genus *NUCLEOPYGUS* Agassiz, 1840

Nucleopygus magnus sp. nov.   Pl. 28, figs 1–7; Figs 71, 72

TYPES. Holotype BMNH EE4339, paratypes, BMNH EE3340, EE3356, EE3358, EE3363, EE3365, EE3367–68, EE4327, EE4335–38

OTHER MATERIAL. An additional 29 specimens were collected. Biometric data was taken from the type series only.

OCCURRENCE. This species was found at the following localities and horizons:

Jebel Buhays, section 1: loose in scree, derived from the lowest few metres of the Simsima Formation (19).

Jebel Buhays, section 3: loose, derived from the lowest bed of the Simsima Formation (1).
Jebel Thanais: lowest 2 m of the Simsima Formation (4).
Jebel Rawdah, section 2: bed 14 (8); loose in scree (3).
Jebel Rawdah, section 4: bed 12 (1).
Jebel Faiyah, section 1b: bed 2 (1).

DIAGNOSIS. A very large, elongate *Nucleopygus* with a deep median depression on the oral surface. The periproct opens relatively close to the posterior border and there is only a short anal sulcus. The posterior petals end at a level slightly anterior to the start of the anal sulcus.

DESCRIPTION. Tests are subquadrate in outline, with a rounded anterior and a somewhat truncated posterior with a shallow anal notch (Pl. 28, figs 1, 4, 5). Test length ranges
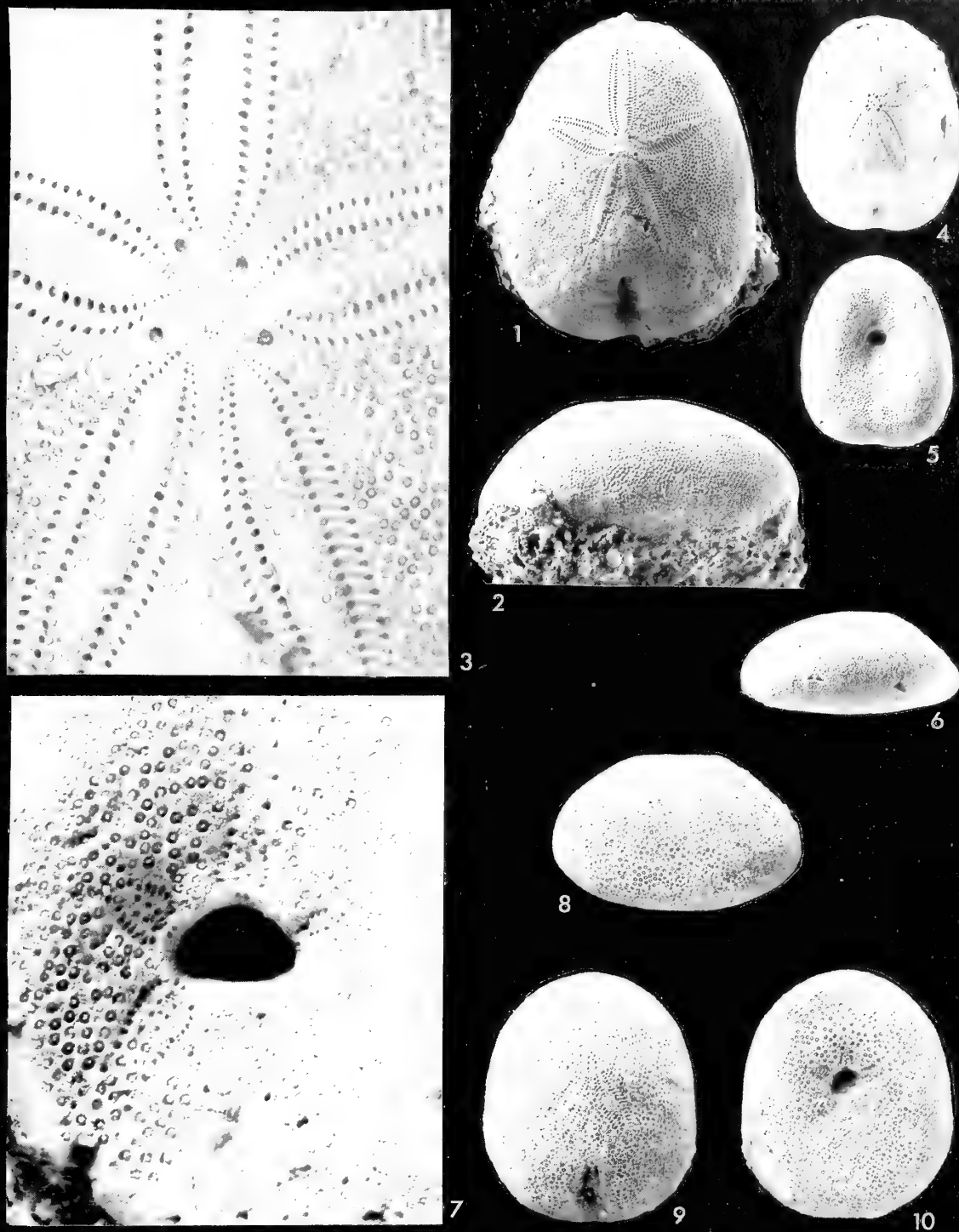
PLATE 28

Figs 1–7 *Nucleopygus magnus* sp. nov. **1–3**, BMNH EE4327, paratype; **1**, apical, × 2; **2**, lateral, × 2; **3**, detail of apical disc, × 4. Jebel Thanais, lowest 2 m of the Simsima Formation. **4–6**, BMNH EE4339, holotype; **4**, apical; **5**, oral; **6**, lateral; all × 1. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation. **7**, BMNH EE3367; detail of peristomial region, × 4. Jebel Buhays, section 2; loose in the scree derived from the lowest 3 m of the Simsima Formation.

Figs 8–10 *Nucleopygus iranicus* (Cotteau & Gauthier). Specimen in the Morgan Collection, Museum d'Histoire Naturelle, Paris; **8**, lateral; **9**, apical; **10**, oral; all × 2. Senonian, Poucht-e-Kouh, Iran.
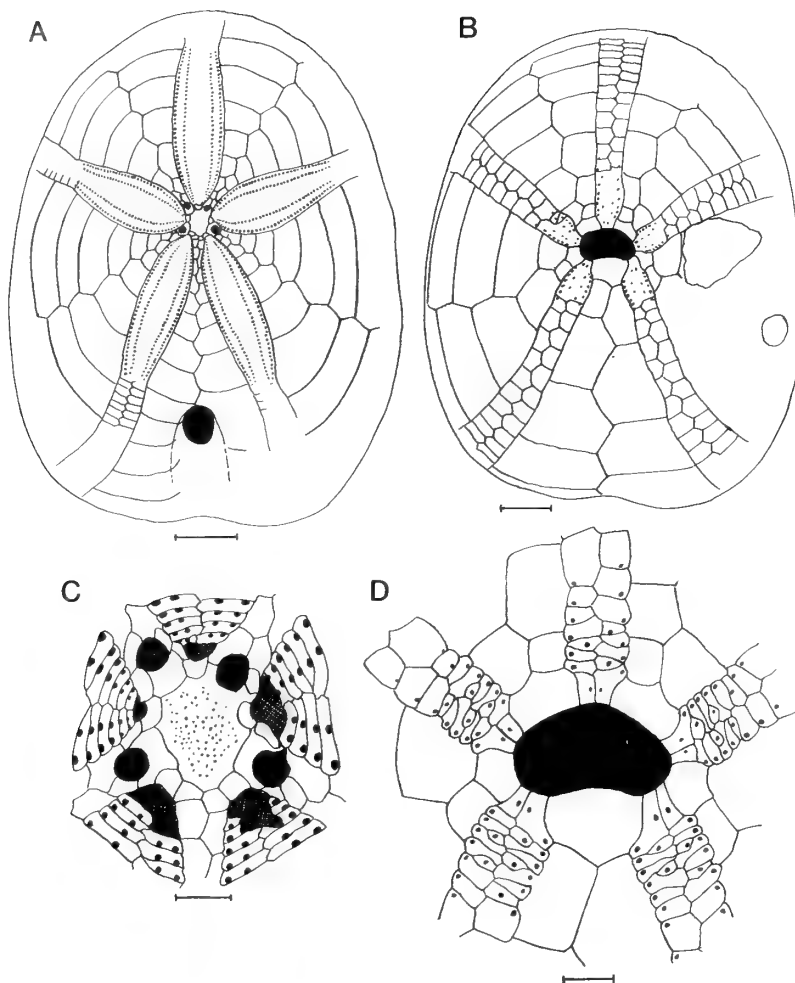
Fig. 72   Camera lucida drawings of plating in *Nucleopygus magnus* sp. nov. **A**, apical surface, BMNH EE4339; **B**, oral surface, BMNH EE4337; **C**, apical disc, BMNH EE4339; **D**, phyllode plating, BMNH EE4337. Scale bars: A, B = 5 mm; C, D = 1 mm.

from 18 mm to about 60 mm (estimated from a broken specimen). Test width is 76–82% of test length (mean = 79%, SD = 2%, N = 11), and the widest point on the test is about two thirds of the distance back from the anterior. The test has a low profile, with test height 42–51% of test length (mean = 39%, SD = 3%, N = 9). It is rounded towards the anterior but obliquely truncated towards the posterior (Pl. 27, figs 2, 6). The ambitus is rounded, but relatively low. The oral surface has a marked median depression and the peristome is sunken (Pl. 28, fig. 5).

The apical disc lies 36–43% of the test length from the anterior border (mean = 39%, SD = 1%, N = 9). It is tetrabasal with large gonopores projecting into the interambulacra (Fig. 72C). Ocular plates are small and U-shaped. The small genital plates are separated from one another by ocular plates.

Petals are open and subparallel to very slightly bowed (lateral and posterior pairs) (Pl. 28, figs 1, 4; Fig. 72A). Pores are both approximately circular and are joined by a well-marked furrow (Pl. 28, fig. 3). The interporal zone is approximately 1·5 times as wide as a pore-zone. The anterior petal is the longest, but is only slightly longer than the posterior petals. It has 30 pore-pairs in a column at 30 mm test length,

rising to 40 at 40 mm test length. The posterior petals end slightly in front of the anal sulcus.

All pores are single below the petals. Phyllodes are hardly expanded adorally (Pl. 28, fig. 7; Fig. 72D). There are buccal pores at the rim of the peristome, situated on relatively short and squat first ambulacral plates. The phyllodes have both an outer and an inner series of pores, although the two series are not well separated (Fig. 72D). There are six pores per column in the outer series in ambulacrum III with 7 or 8 in the other ambulacra, and 1 or 2 pores in the inner series of ambulacrum III with 2 or 3 in other ambulacra. Every third ambulacral plate is occluded, but the occluded plates do not form a continuous inner series. The phyllodes are not depressed relative to the surrounding test. There are no bourrelets, but the walls to the peristome are covered with fine, dense tubercules. The posterior interambulacrum differs from other interambulacra in that it does not turn sharply in towards the peristome, but instead forms a sloping shelf into the opening.

The peristome is pentagonal in outline, approximately 1·6 times as wide as long. It lies 38–42% of the test length from the anterior border (mean = 40%, SD = 1%, N = 10).

The periproct is tall and narrow and has a width approximately 40% of its height. It opens into a narrow, parallel-

sided anal sulcus that slopes posteriorly. The periproct opens 73–85% of test length from the anterior border (mean = 78%, SD = 4%, N = 11).

The upper surface is covered in fine, slightly sunken tubercles. Adorally tubercles are coarser but are still sunken. There is a narrow, zig-zagged granular zone in the posterior interambulacrum that follows the interradial suture and tapers out before reaching the pesterior border (Pl. 27, fig. 7). It is never more than about 78% of the test width at its widest.

REMARKS. Few other species of *Nucleopygus* come anywhere near the size of *N. magnus*. Both *N. iranicus* (Cotteau & Gauthier) (Pl. 28, figs 8–10), from the late Cretaceous of southern Iran, and *N. pullatus* Stolizcka, from the Maastrichtian of southern India are much smaller species, reaching little more than 14 mm in test length. Furthermore, they are squatter. *N. geayi* (Cottreau), from the Maastrichtian of Madagascar, is even smaller, never being reported larger than 8 mm test length. Similarly, the European species *N. coravium* and *N. scrobiculatus* are equally small forms.

Only in the late Cretaceous of North Africa do any *Nucleopygus* approach the size of *N. magnus*. *N. inaequalis* (Peron & Gauthier) resembles *N. magnus* in shape but its posterior petals extend posteriorly beyond the start of the anal sulcus. *N. meslei* (Peron & Gauthier), from the Campanian, is probably the closest. *N. meslei* reaches 30 mm in test length, but differs from *N. magnus* in having a more anterior apical disc, a longer anal sulcus and more petaloid ambulacra. It is also less markedly depressed along the midline on the oral surface.

Family ECHINOLAMPADIDAE Gray, 1851
Genus *ARNAUDASTER* Lambert, 1918

REMARKS. Until now there has only been one species assigned to this genus, *A. gauthieri* Lambert, from the Cenomanian of France (Aquitaine). Kier (1962: 105) noted that *Arnaudaster* might best be considered a synonym of *Parapygus*, as it differs only in having a more cylindrical shape and more unequal poriferous zones in the same petal. The discovery of a Maastrichtian species very close in form to *A. gauthieri* supports the maintenance of *Arnaudaster* as a separate genus. *Pseudocatopygus longior* Cotteau & Gauthier, from the late Cretaceous of Iran, also has unequal columns in its petals and may belong to *Arnaudaster*. However, Kier (1962) placed *Pseudocatopygus* as a synonym of *Parapygus*.

Arnaudaster cylindriformis sp. nov.   Pl. 25, figs 11, 12; Pl. 29, figs 1–9; Figs 73–75

TYPES. The holotype is BMNH EE4334, paratypes are BMNH EE4324, EE4331–33, EE3378–81.

OTHER MATERIAL. Three poorly preserved specimens, BMNH EE3374–76. BMNH EE3373 may also belong here, but only a fragment of the upper surface is preserved and this apparently shows equally developed columns of pore-pairs in ambulacrum petal V.

OCCURRENCE. This species was found at the following localities along the western margin of the Oman Mountains:
Jebel Buhays, section 1: top of bed 1 (1); loose in the scree,
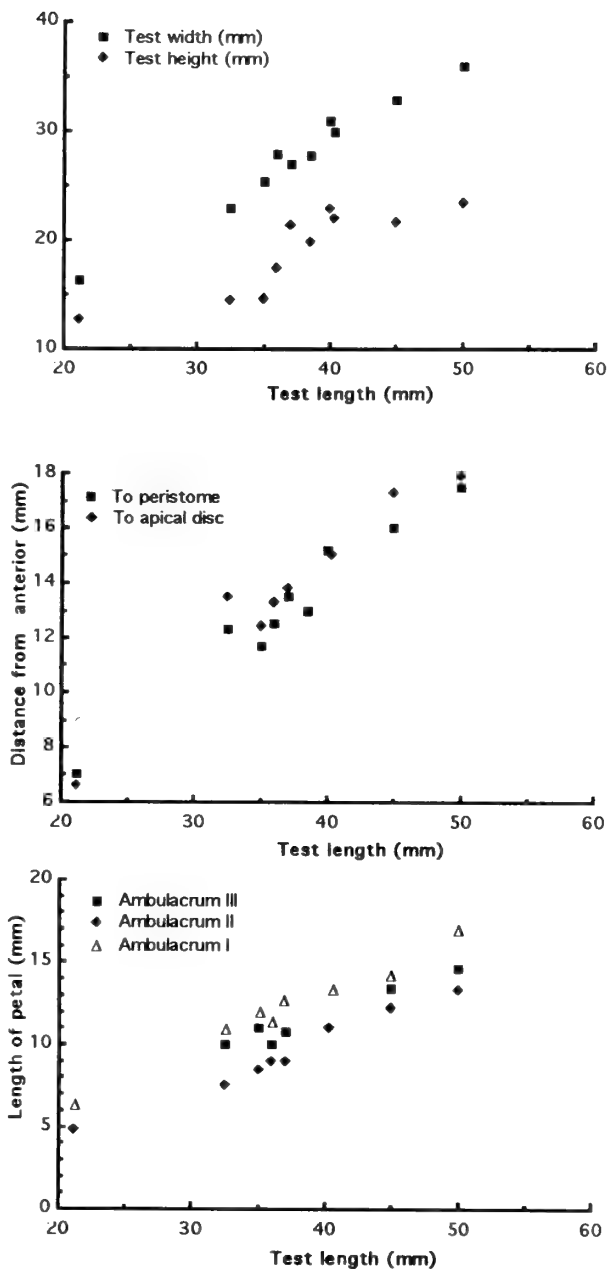
Fig. 73   Biometric data for *Arnaudaster cylindriformis* sp. nov.

derived from the lowest few metres of the Simsima Formation (6).
Jebel Rawdah, section 2: bed 14 (1); loose at the level of bed 19 (2); loose in scree, derived from beds 14–21 (2); bed 21 (1); bed 26 (1).
Jebel Rawdah, section 3: bed 9 (1); loose near top of section (1).

DIAGNOSIS. An *Arnaudaster* with a wide, pentagonal peristome with weak bourrelets and approximately four pores in the inner series of phyllodes in each half ambulacrum.

DESCRIPTION. Tests range from 21 to approximately 50 mm in length, although many specimens are lacking the very
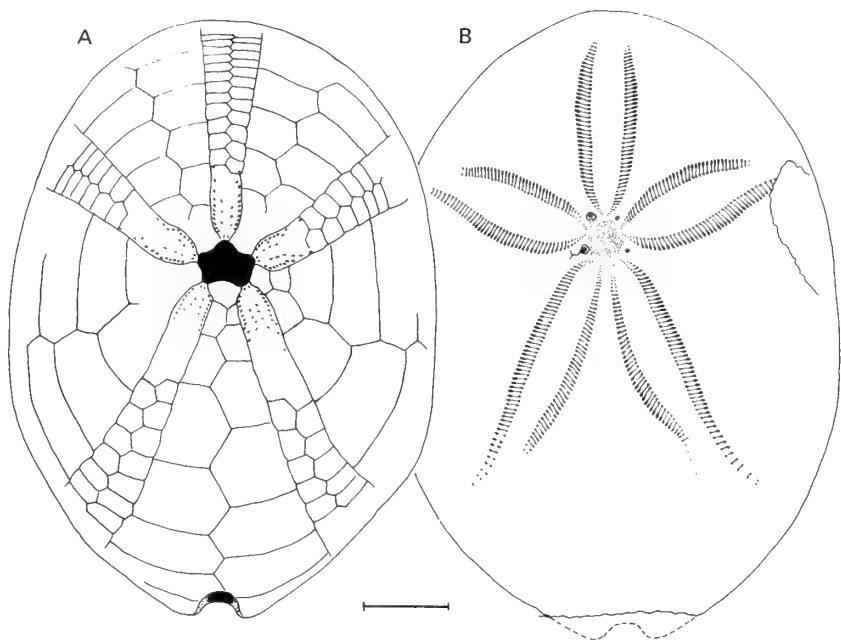
Fig. 74 Camera lucida drawing of plating in *Arnaudaster cylindriformis* sp. nov, **A,** oral surface, BMNH EE4324; **B,** apical surface, BMNH EE4333. Scale bar = 5 mm.
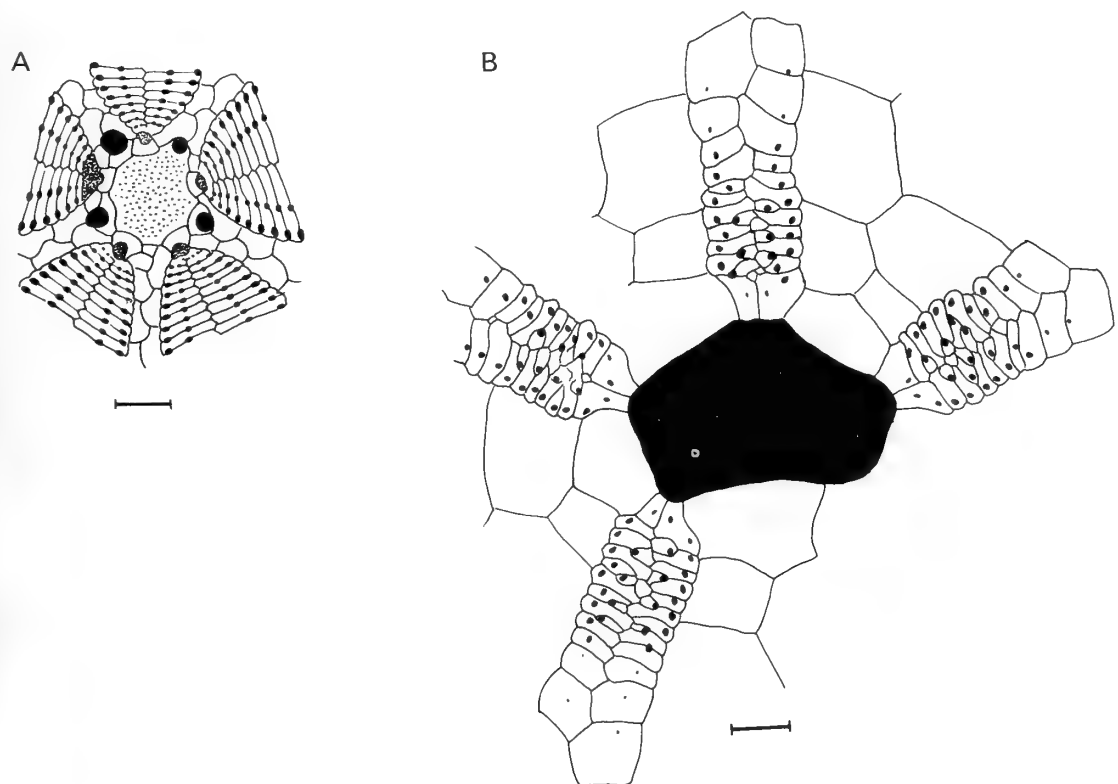
Fig. 75 Camera lucida drawings of plating in *Arnaudaster cylindriformis* sp. nov. **A,** apical disc, BMNH EE3379; **B,** phyllode plating, BMNH EE4324. Scale bars = 1 mm.

posterior end of the test. Tests are ovoid in outline with a rounded anterior and a very weakly pointed posterior (Pl. 25, figs 11, 12; Pl. 29, figs 1, 8). Test width is 71–78% of test length (mean = 74%, SD = 2·5%, N = 10), with the widest point on the test approximately two thirds of the distance from the anterior and well behind the level of the apical disc. Test height is 41–60% of the length (mean = 51%, SD = 6·1%, N = 10). In profile the upper surface is broad and almost flat, uniformly rounded at the anterior, but undercut at the posterior (Pl. 29, figs 4, 7, 9). The oral surface is flat or very slightly sunken towards the peristome, while the ambitus is smoothly rounded.

The apical disc lies well anterior of centre, some 31–41% of test length from the anterior border (mean = 37%, SD = 2·9%, N = 8). Plating is tetrabasal, although genital plate 2 is enormously enlarged in comparison to the other genital plates and occupies the centre of the disc (Fig. 74A). The entire madreporic plate is covered in dense, fine perforations. Other genital plates are very small and are dominated by the gonopores. There may be sexual dimorphism in the size of gonopore openings. Ocular plates are small, approximately the same size as the genital plates.

Ambulacra are petaloid with the interporal zone slightly inflated. The anterior and two posterior petals are similar in size, but the lateral petals are shorter. Petals are broad, lanceolate with more or less parallel columns of pore-pairs at the distal tip (Pl. 29, fig. 2; Fig. 74B). They extend about 80% of the distance to the ambitus. Pore-pairs are conjugate. The anterior petal has columns of equal length, with 41 pore-pairs in a column at 32 mm test length, rising to 57 at 50 mm test length. The anterior column of pore-pairs in the lateral petals is shorter than the posterior column by about five pore-pairs (Fig. 74B). Distally they are slightly narrower, but remain broadly open. The posterior petals also have unequally developed columns of pore-pairs, with the posterior column shorter than the anterior column by seven or so pore-pairs. They extend approximately 70% of the distance to the ambitus and remain broadly open distally.

Below the petals pores are single. Phyllodes are not strongly developed and phyllode plating is best seen in BMNH EE3379. Pores of the outer series become enlarged close to the peristome, but the rows of pores do not bow out (Fig. 75B). There are only eight or nine pores forming the outer series in one half ambulacrum. There are three or four pores forming an inner series in each half ambulacrum. Each inner series pore is found on an occluded plate (Fig. 75B). There are small but obvious buccal pores which are not separated from the other pores of the phyllode but which open right at the peristomial rim.

The first interambulacral plates are short and wide and are slightly swollen to form a weak floscelle (Pl. 29, fig. 3; Fig. 75B). The peristome is pentagonal, approximately twice as wide as long, and with well-developed vertical walls.

The periproct is small and transversely oval, with a width approximately 50–70% of its height. It lies at approximately mid-height on the posterior face, but is angled slightly downwards so that it is just visible from the oral surface and not from the adapical surface (Pl. 29, figs 5, 8). Because the posterior of the test is slightly drawn out, the periproctal region is often damaged. The base of the periproct lies between about 30 and 40% of the test height above the base. Tubercles are small, sunken and densely crowded over the whole surface.

REMARKS. This species comes very close to the type species A. gauthieri in almost every respect. Both have a very similar, cylindrical test, anterior apical disc and strongly unequal columns of pores in both lateral and posterior petals (the same columns that are asymmetric). The only difference of significance appears to be in the development of phyllodes. In A. gauthieri the inner series of pores is rather poorly developed and not well separated from the outer series. In A. cylindriformis the inner series pores are somewhat more numerous and form a distinct series. However, this is a minor difference, and there is very little else to separate the two forms.

The species also resembles Parapygus inflatus Cotteau & Gauthier in its overall shape and appearance. However, Cotteau & Gauthier catagorically state (1895: 55) that the columns of pore-pairs in the petals of the species are equally developed.

Order **HOLASTEROIDA** Durham & Melville, 1957
Family **HOLASTERIDAE** Pictet, 1857
Genus *HEMIPNEUSTES* Agassiz, 1836

DIAGNOSIS. Heart-shaped holasteroids showing pronounced petal asymmetry, with the posterior column of pores well developed and anterior column rudimentary. Periproct sub-ambital and clearly visible in oral view because of the distinct posterior notch. The madrepores extend over all genital plates as well as the anterior three ocular plates. Plastron plates wedge-shaped, each just reaching the opposite adradial suture and thus biserially arranged.

OCCURRENCE. Late Campanian and Maastrichtian, Europe, North Africa and the Middle East.

REMARKS. *Hemipneustes* is very close in appearance to *Cardiaster*. Both have a cordiform test with a deep, well-defined anterior sulcus which has enlarged primary tubercles along its border. Both genera also have a similar style of plastron plating, composed of a short, broad labral plate followed by up to five wedge-shaped plates which more or less occupy the full width of the plastron (eg. Ernst 1972, text-fig. 20). Finally, both have rather similar petals, with the anterior column greatly reduced in comparison to the posterior column. The primary difference between *Cardiaster* and *Hemipneustes* lies in the fact that *Hemipneustes* has little more than rudimentary pore-pairs in the anterior columns of its petals, whereas *Cardiaster* has small but distinctly conjugate pore-pairs in these anterior columns. Furthermore, madrepores are more extensively developed in *Hemipneustes*, extending beyond genital plate 2 to cover genital plate 3 and ocular plates II, III and IV.

Many species names have been erected in the past, mostly based on relatively few specimens and often on rather poorly preserved material. From Noetling (1897) onwards workers have relied on two simple biometric indicators to distinguish species of this genus; width/length and height/length ratios (see for example Devries 1967; Aziz & Badve 1990). However, not only do these ratios vary ontogenetically and thus vary according to absolute test size, but they have also rarely been applied rigorously using large populations.

There are three species found amongst the material collected from the Oman Mountains. These appear to have some stratigraphic value. The lowest forms found at Jebel Rawdah belong to *H. persicus* var. *sardanyolae* Vidal, and

are found in the basal sandy facies. These have the broad shallow anterior sulcus characteristic of the *H. delettrei* complex, a group restricted to the late Campanian of Tunisia and Algeria (Zhagbib-Turki 1987). Above this, or possibly partially overlapping, *H. arabicus* is found. This species is similar in profile and in the positioning of its apical disc, but has a much narrower, deeper and more sharply defined anterior sulcus. The first elevated *Hemipneustes* forms, belonging to *H. compressus,* appear in bed 14, having more uniformly rounded profiles. However, by the time bed 21 is reached, *H. compressus* has a much more quadrate profile with strongly pinched ridges to the frontal groove. Finally, by bed 26 some *H. compressus* appear that are very elevated and which have developed a strong slope towards the posterior similar to the late Maastrichtian *H. striatoradiatus.*

In trying to identify the Oman/United Arab Emirates species, a number of other species have been examined and the following are accepted as valid:

Hemipneustes delettrei Peron & Gauthier (Pl. 30, figs 9, 10), late Campanian of Algeria. Rounded in outline and variable in profile, from highly inflated (*H. africanus* form) to depressed (*H. delettrei* form). w/l = 0·89–0·95 (mean = 0·91): h/l = 0·58–0·79 (mean =0·70) [size range 73–98 mm]. Distinguished from all other species by the large, broad anterior ambulacral sulcus; about twice as broad as in any other species.

Hemipneustes striatoradiatus (Leske) (Pl. 30, figs 7, 8; Fig. 78C), Upper Maastrichtian of the Netherlands. Rounded in outline with a very narrow and shallow anteal sulcus. Variable in profile from flat-topped to distinctly raised anterior to the apical disc. Sides rather vertical giving quadrate cross-section. Apical disc anterior of centre. w/l = 0·87–0·97, mean = 0·91: h/l = 0·61–0·80, mean 0·69 [Size range 50–100 mm]. Distinguished from other species by (i) its narrow, shallow anteal sulcus, (ii) rounded outline and (iii) quadrate lateral cross-section.

Hemipneustes pyrenaicus Hebert (Pl. 30, figs 5, 6) – closest to *H. compressus* in having a short narrow frontal groove with a strong vertical component, anterior apical disc, and quadrate profile. It differs in having a flat apical surface and in lacking adapical pinched ridges to the anterior sulcus.

H. persicus Cotteau & Gauthier (Pl. 31, figs 1–7; Pl. 32, figs 1–4; described below).

H. compressus Noetling (Pl. 31, figs 8–11; described below).

H. arabicus Ali (Pl. 30, figs 1–4; described below).

In addition the following species are treated as synonyms or rejected names, or are based on inadequate material:

H. minor Peron & Gauthier, Upper Senonian of Iran (a small *H. persicus* Peron & Gauthier).

H. oculatus Cotteau, Maastrichtian of Ciply, Belgium. This appears to be a large variety of *H. striatoradiatus,* somewhat crushed but with a deeper frontal groove as illustrated by Cotteau. The specimens referred to under this name by van der Ham (1989) are simply rather tall and posteriorly inclined *H. striatoradiatus.*

H. arnaudi Cotteau 1892, Upper Senonian of Dordogne. This is very like high forms of *H. compressus* in having an elevated keel to the ambulacrum. It has too wide an anterior sulcus to be a *H. striatoradiatus.* Treat as a probable synonym.

H. indicus Aziz & Badve 1990; Maastrichtian of S India, is identical in profile to *H. arnaudi* but larger. Its deep frontal groove and anterior apical disc makes it part of the *compressus* group.

H. sardanyolae Vidal 1921, Campanian of Spain, is treated here as a shallow grooved variety of *H. persicus.*

H. nicklesi Vidal 1921, Campanian of Spain, is a *Hemipneustes* sp. based on crushed and badly preserved specimens that are basically indeterminate. It is probably a synonym of *H. persicus* var. *sardanyolae* Vidal.

Spatangoides martelli Checchia-Rispoli, Maastrichtian of Libya. Here synonymized with *H. compressus* Noetling.

Spatangoides tripolitanus Checchia-Rispoli, Maastrichtian of Libya, is clearly a species of *Opisopneustes.* Its primary adapical interambulacral tubercles are well developed and it represents a valid species, differing from *O. cossoni* in having a vertically positioned periproct.

Spatangoides aichinoi Checchia-Rispoli, Maastrichtian of Libya. Here synonymized with *H. persicus.*

Hemipneustes batheri Lambert [=*H. leymeriei* Noetling]. This is probably a variety of *H. persicus,* having the posterior apical disc and oval outline with shallow and open anterior sulcus, but it is unusually tall.

H. noetlingi Lambert was erected as a replacement name for *H. pyrenaicus* of Noetling, from the Maastrichtian of Baluchistan. However, like Devries (1967), I can find no significant difference between Noetling's specimens and the type material of *H. pyrenaicus* and treat *H. noetlingi* as a junior synonym.

Hemipneustes leymeriei Hebert has the very narrow and shallow groove and circular outline of a *H. striatoradiatus.* Topotype material from Gansec, southern France, confirms this.

Spatangoides tripolitanus Checchia-Rispoli is a species of *Opisopneustes.*

Hemipneustes compressus Noetling, 1897　　Pl. 31, figs 8–11; Figs 76, 77, 78A

1897　*Hemipneustes compressus* Noetling: 34, pl. 7, figs 3, 4, pl. 8, figs 1, 2.

1931　*Spatangoides Martellii* Checchia-Rispoli: 7, pl. 1, figs 1–3.

1967　*Hemipneustes compressus* Noetling; Devries: 188, pl. 6, figs 31–33.

TYPES. The syntypes are the four specimens illustrated by Noetling and presumably in the Geological Survey of India collections.

MATERIAL STUDIED. Thirty specimens were collected. Biometric data was taken from the following 16 specimens: BMNH EE3744–45, EE3748, EE4070–71, EE4073–74, EE4076, EE4078–82, EE5022–24.

OCCURRENCE. Maastrichtian of Libya, Oman and Baluchistan. In the western Oman Mountains it occurs at the following levels:

Jebel Rawdah, section 2: bed 14 (2); bed 15 (2); bed 19 (1); beds 20/21 (17); bed 22 (1); bed 26 (2 specimens plus fragments); bed 27 (2).

Jebel Rawdah, section 3: beds 9/10 (1).

Jebel Rawdah, section 4: loose, towards top of section (1).

DIAGNOSIS. Test rather more elongate than in other species, typically flat-topped in side-view and arched in cross-section.
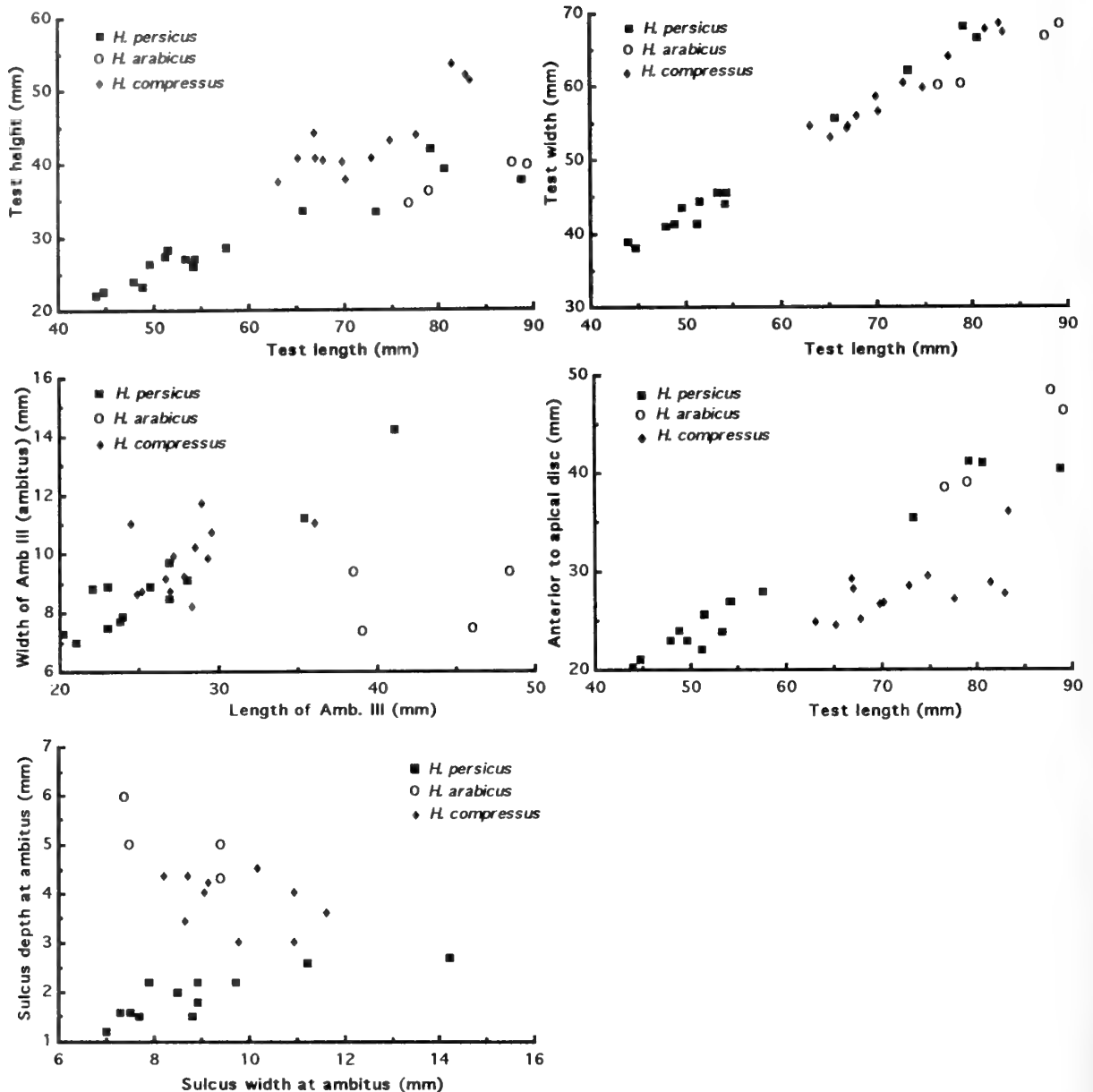
Fig. 76 Biometric data for species of *Hemipneustes*.

w/l = 80–87% of length, mean = 83%; height 54–67% of length, mean = 60% (size range 63–83 mm). Frontal groove narrow but moderately deep at the anterior; typically slightly keeled. Apical disc lies well towards the anterior (distance between anterior and apical disc = 34–44% of length: mean = 39%) and is pinched up. Distinguished from other species by (i) its anterior apical disc, (ii) the deep anterior groove which is relatively short and geniculate with a strong vertical component, (iii) being more subquadrate outline, typically inclined from the apical disc posteriorly.

DESCRIPTION. Tests range in length from 63 to 83 mm in length and from 53 to 69 mm in width (width = 80–87% of length; mean = 83%, SD = 1·8%, N = 13). In outline the test is cordate with a sharp, deep anterior sulcus, and a

truncated and even slightly indented posterior (Pl. 31, figs 8, 9). The widest point on the test lies approximately mid-length. Test height is variable, ranging from 38 to 54 mm (height = 54–66% of test length: mean = 60%, SD = 3·7%, N = 13). In side view the upper surface varies from almost flat to strongly vaulted, with the tallest point on the test lying immediately anterior of the apical disc (Pl. 31, fig. 11). The test slopes towards the posterior which is truncated. Anterior to the apical disc the test curves uniformly to become almost vertical. There is a sharp curve from the anterior to the more or less flat base (Pl. 31, fig. 11). In anterior profile the test appears vaulted with rounded sides sloping up to the crest. The anterior sulcus becomes slightly pinched towards the base and its edges are sharply delimited (Pl. 31, figs 10, 11).
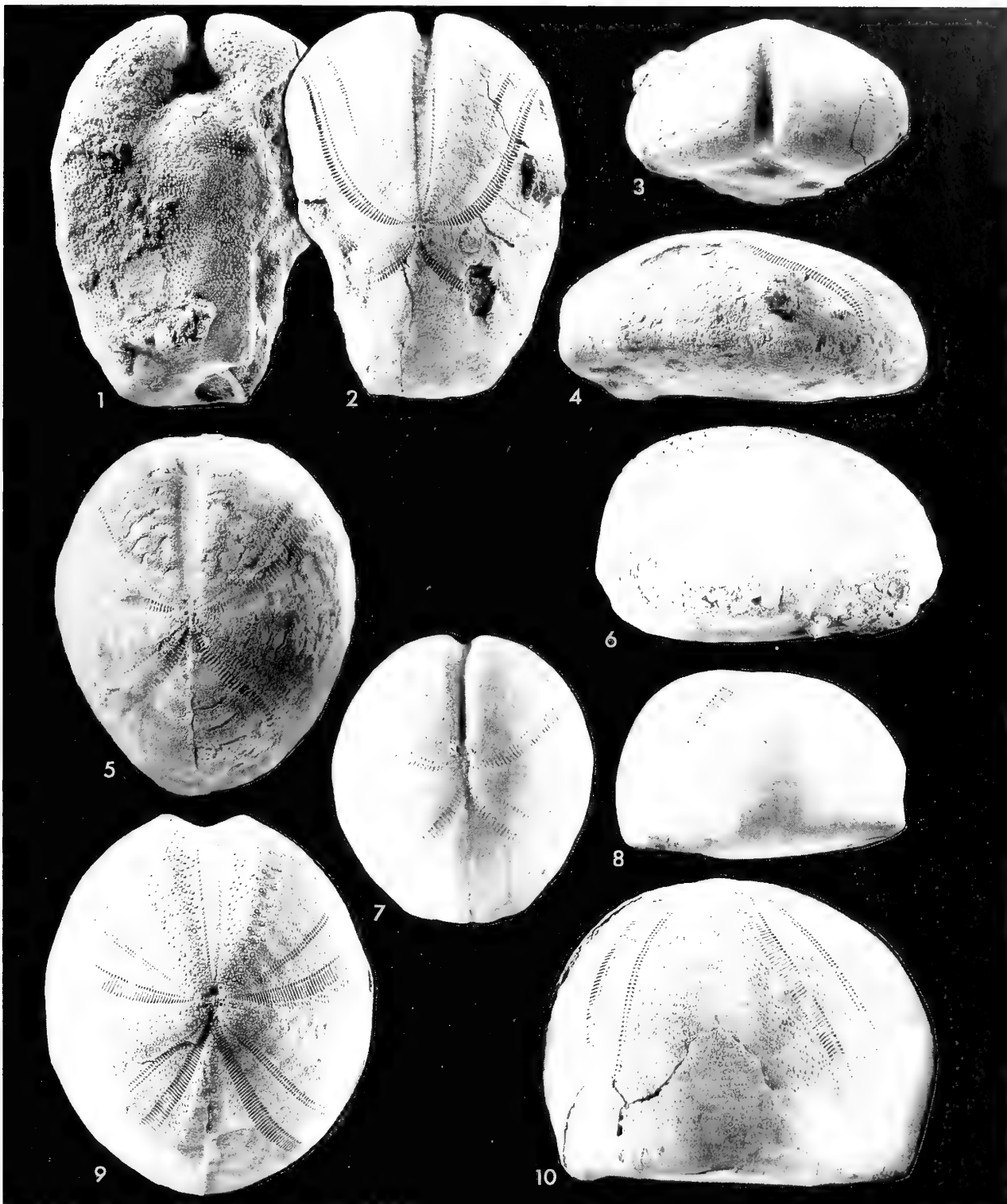
PLATE 30

Figs 1–4 *Hemipneustes arabicus* Ali. BMNH EE5027; **1**, oral; **2**, apical; **3**, anterior; **4**, lateral; all × 1. Jebel Rawdah, section 1, bed 4.

Figs 5, 6 *Hemipneustes pyrenaicus* Hebert. Specimen in the Museum d'Histoire Naturelle, Paris; Maastrichtian of Montbéraud, Haute Garonne, France. **5**, apical; **6**, lateral; both × 1.

Figs 7, 8 *Hemipneustes striatoradiatus* (Leske). BMNH 75822; **7**, apical; **8**, lateral; both × 1. Maastrichtian of Maastricht, The Netherlands.

Figs 9, 10 *Hemipneustes delettrei africanus* Peron & Gauthier. BMNH E3654; **9**, apical; **10**, lateral; both × 0·75. Upper Campanian of Ain Joutu, Algeria.
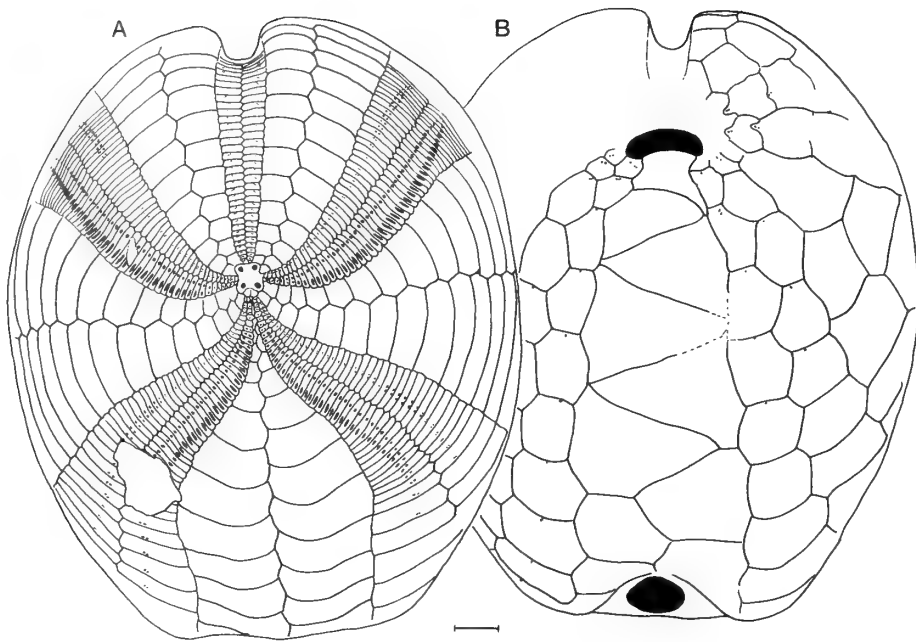
Fig. 77 Camera lucida drawings of plating in *Hemipneustes compressus* (Noetling), BMNH EE3745. **A,** apical surface; **B,** oral surface. Scale bar = 5 mm.
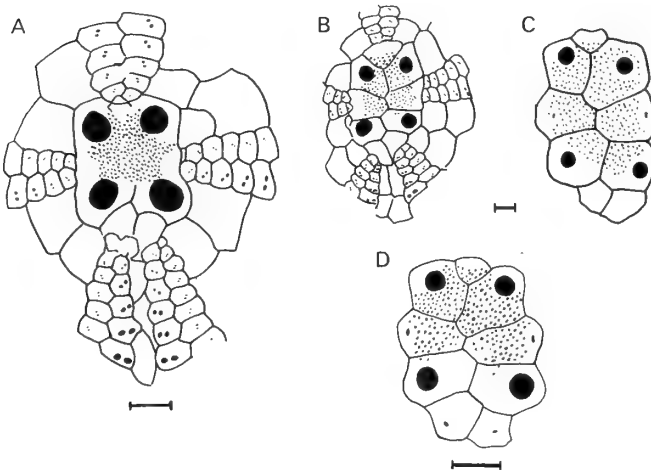
Fig. 78 Camera lucida drawings of apical disc plating in species of *Hemipneustes*. **A,** *H. compressus* (Noetling), BMNH EE3745; **B,** *H. arabicus*, BMNH EE5027; **C,** *H. striatoradiatus* (Leske), BMNH 38630; **D,** *H. persicus* Cotteau & Gauthier, BMNH EE3747. Scale bars = 1 mm.

The apical disc lies at or slightly in front of mid-length (distance to the anterior border = 34–44% of test length: mean = 39%, SD = 3·1%, N = 13). It is elongate with 4 gonopores occupying most of the area of the genital plates (Fig. 78A). The anterior pair of genital plates are separated from the posterior pair by the lateral ocular plates. Madrepores extend across genital plates 2 and 3, as well as ocular plates II, III and IV, even extending into the wall of the gonopores in some instances. The two posterior ocular plates are slightly larger and abut each other.

The anterior ambulacrum is non-petalloid. It is almost flush at the apex, becomes slightly depressed towards the anterior and then forms a deep vertical sulcus close to the anterior (Pl. 31, figs 8, 10). This groove continues up to the peristome and is widest near the top of the anterior sulcus becoming narrower towards the base of the sulcus. Pore-pairs are oblique isopores, closely spaced in the upper half, but becoming smaller and more widely spaced towards the bottom of the sulcus. The margins of the sulcus are relatively sharp, especially towards the top of the anterior sulcus, where they may form small crests on either side. The width of the sulcus is 13–20% of the test width (mean = 16·3%, SD = 1·86%, N = 12) and at its deepest it is about 3·5 to 4·5 mm.

The anterior petals are strongly asymmetric, with only the posterior column well-developed (Pl. 31, fig. 8; Fig. 77). These curve forward and, towards the tip, turn slightly down. The inner pore is circular, the outer one elongate, and the distance between the pairs is as wide as the outer slit-like pore. Pore-pairs are conjugate and are separated from one another by a single row of small tubercles. The posterior column tapers both adapically and adambitally. There are 45 pore-pairs in a column in a 65 mm individual, rising to 52 in an 81 mm individual (Fig. 76). The anterior column of pores remains rudimentary throughout. All are pore-pairs, but the pores always remain small and close together, never becoming conjugate. However, they do gradually increase in size towards the ambitus.

The posterior petals are similar to the anterior petals in their pore-pair development and column asymmetry, with only the posterior column bearing large conjugate pore-pairs (Fig. 77). This column is flexed outwards and backwards and extends only about two thirds of the distance towards the ambitus. There are 32 pore-pairs in a column in a 65 mm individual, rising to 42 in an 81 mm individual. Close to the apex the two ambulacra are almost parallel, but further away they diverge at about 90°. Pores beneath the petals remain double, but are microscopic. Close to the mouth there are

two to three larger peribuccal pores in ambulacrum III, four to five in ambulacra II and IV, and three to four in ambulacra I and V.

The interambulacra are biserial to the apex, although they become extremely narrow, especially posteriorly. On the oral surface there is a short, broad labral plate followed by a series of 5 alternating triangular-shaped plates which either just or almost reach the opposite suture (Fig. 77). Further towards the posterior the columns become more typically biserial.

The peristome is oval, slightly more than twice as wide as long, and lies at the base of the anterior sulcus, some 15–18% of test length from the anterior (mean = 17%, SD = 1·2%, N = 11). The peristome faces forward and is visible in anterior view. The labral plate hardly indents the posterior of the peristome.

The periproct is oval, typically about 70% as wide as tall, and is strongly overhung so that it is visible from the oral surface but not from the apical surface (Pl. 31, figs 8, 9). The test beneath the periproct is indented and there are two projections on either side. The periproct opens between interambulacral plates 5 and 10, the lower plates being strongly curved. The periproct lies low on the posterior surface and the distance to the base of the periproct from the lower surface is some 18–27% of the test height.

Tuberculation is fine and uniform throughout, except along the inner (interambulacral) margin of the frontal sulcus where a double or triple row of noticeably larger tubercles is developed. There is no trace of a lateral fasciole to be seen. Oral tubercles are slightly larger than adapical ones, but there is no real difference in size between the tubercles of the plastron and those of the latero-ventral regions. The oral ambulacra appear to be tubercle-free.

REMARKS. This species is relatively common at certain levels in Jebel Rawdah. It co-occurs with small varieties of *H. persicus* but can be distinguished from that species by its narrower, more vertical and more sharply defined anterior sulcus, its more anterior apical disc, its lack of adapical primary tubercles, and its more quadrate profile. It differs from *H. arabicus*, whose size range is more-or-less coinci-

dent, in having the apical disc positioned anterior of centre, and in having a more developed vertical component to the anterior sulcus.

The stratigraphically lowest species tend to have a more rounded profile, while higher samples become progressively more peaked, with a stronger posterior inclination as the region immediately in front of the apical disc becomes taller. Thus in the beds immediately above bed 13, Jebel Rawdah, section 2, *H. compressus* is rather flat and the vertical component of the anterior sulcus is small. By bed 21 the tests are much more quadrate in outline, with a small but obvious peak in front of the apical disc, and by bed 26 some highly elevated tests are found.

Hemipneustes persicus Cotteau & Gauthier, 1895   Pl. 31, figs 1–7; Pl. 32, figs 1–4; Figs 76, 78D, 79

1895 *Hemipneustes persicus* Cotteau & Gauthier: 15, pl. 2, figs 1–6.
1895 *Hemipneustes minor* Cotteau & Gauthier: 17, pl. 2, figs 7–9.
1921 *Hemipneustes sardanyolae* Vidal: 11, pl. 2, fig. 2; pl. 3, fig. 2.

TYPES. The syntypes are the specimens from Aftab and Derre-i-Chahr, Iran, described by Cotteau & Gauthier (1895: 15). Although the authors stated that they had many examples, their description appears to have been based on only one specimen 54 mm in length, which was illustrated. This is here designated lectotype.

MATERIAL STUDIED. There are five large individuals of this species, BMNH EE4083, EE4084, EE4090, EE5025–26, all rather poorly preserved. Small individuals that appear indistinguishable are relatively common and well-preserved at one horizon at Jebel Rawdah, section 2. Biometric data is based on the following eleven specimens: BMNH EE3742, EE3746–47, EE4091, EE4097, EE4099, EE5028–32 in addition to the five larger specimens cited above.

OCCURRENCE. In the Oman Mountains region this species
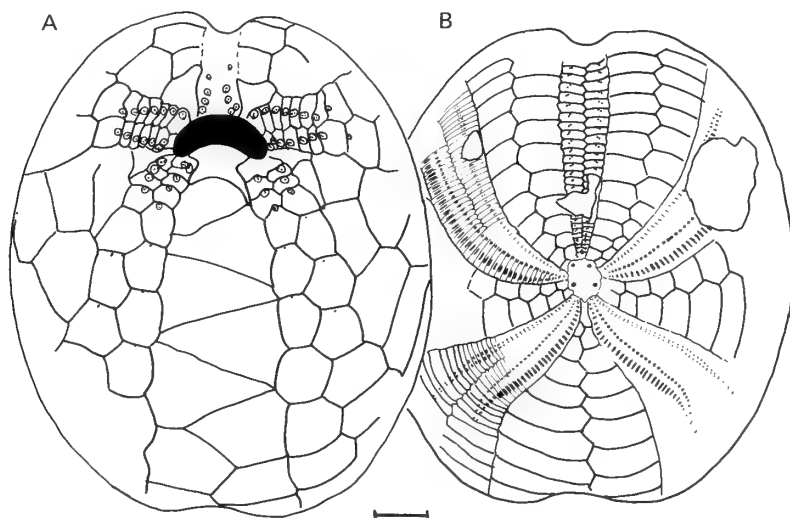
Fig. 79 Camera lucida drawing of plating in *Hemipneustes persicus* Cotteau & Gauthier. **A,** oral surface, BMNH EE3747; **B**, apical surface, BMNH EE3746. Scale bar = 5 mm.

occurs at Jebel Rawdah at the following localities and horizons:

Section 1: bed 4 (2).

Section 2: bed 19 (1); beds 20/21 (23); loose in scree, derived from beds 14–21 (4).

Section 3: bed 5 (1); bed 7 (1).

Section 4: loose a little below the top of the measured section (1).

The type series comes from the 'Senonienne' (probably Maastrichtian) of Aftab and Derre-i-Chahr, southern Iran.

DIAGNOSIS. Test ovate, depressed in side-view and in cross-section arched. Width 80–88% of length, mean = 85%: height 42–55% of length, mean = 49% [size range 44–89 mm test length]. Frontal groove broad and open, expanding anteriorly, comparatively shallow at the anterior; never keeled. Apical disc lies approximately mid-length (distance between anterior and apical disc 45–52% of test length; mean = 48%). Distinguished from other species by (i) its depressed, rounded profile, (ii) broad, relatively shallow anterior groove (iii) central apical disc.

DESCRIPTION. Tests range from 44 to 89 mm in length and from 38 to 68 mm in width (width = 80–88% of length; mean = 85%, SD = 2·1%, N = 4). In outline the test is oval with a prominent anterior sulcus and a truncated posterior (Pl. 31, figs 1, 3, 4, 6). The widest point on the test is approximately mid-length. In profile the test is depressed, more or less uniformly curved both in front and behind, with the tallest point of the test anterior of centre (Pl. 31, figs 2, 5). Test height is 42–53% of length (mean = 48%, SD = 4·2%, N = 5). In anterior profile the sides are uniformly rounded.

The apical disc lies approximately mid-length, 43–52% of test length from the anterior border (mean = 48%, SD = 2·4%, N = 15). Plating appears to be similar in arrangement to that of *H. compressus*, with the anterior pair of genital plates separated from the posterior pair by ocular plates II and IV, which meet centrally (Fig. 78D). Madrepores extend over genital plates 2 and 3, and over ocular plates II, III and IV.

The pores of the anterior groove are small and closely spaced adapically, becoming slightly more widely separated towards the ambitus. The anterior sulcus is rather broad and shallow, becoming more or less parallel-sided towards the anterior border (Pl. 31, figs 1, 3, 6). The margins of the groove are gently rounded, never crested. The width of the sulcus is 17–22% of the test width (mean = 19%, SD = 2·0%, N = 13) and at its deepest it is only 2·0–3·0 mm in depth. The sulcus does not have a vertical component at the anterior, as is seen in *H. compressus*, but curves uniformly towards the ambitus.

Petals are as in *H. compressus*, though the anterior pair are slightly more curved forwards than in that species (Fig. 79). The anterior column of pore-pairs in each petal is composed of small, rudimentary pore-pairs which become slightly larger towards the ambitus. The posterior column in each petal is composed of wide, conjugate pore-pairs, with the inner pore circular and the outer pore distinctly slit-like. There are 36 pore-pairs in the posterior column of ambulacrum II petal, and 28 in ambulacrum I petal in a 44 mm length individual, rising to 65 and ?55 pore-pairs respectively in an 80 mm individual. The anterior petals curve forwards to diverge at an angle of approximately 30° to the midline, before tapering

and turning laterally slightly at their distal end. They extend almost to the ambitus in adapical view (Fig. 79). The posterior petals are slightly shorter, extending approximately two-thirds of the distance to the ambitus. They too are flexed, but for most of their length they diverge at approximately 50° to the midline. Pores below the petals are microscopic, but remain double. Peribuccal pores are well-developed, with four or five to a column in ambulacrum III, six or seven in ambulacra II and IV, and four or five in ambulacra I and V.

The interambulacra become very narrow adapically (Fig. 79), but remain biserial. The plastron consists of a small, broad, labral plate followed by five wedge-shaped plates arranged uniserially (Fig. 79).

The peristome is oval to crescentic, slightly more than twice as wide as long, and lies at the base of the anterior sulcus, some 17–21% of test length from the anterior (mean = 19%, SD = 1·8%, N = 5). The labral lip projects downwards slightly and is visible in anterior view. The labral plate indents the posterior of the peristome.

The periproct is oval, 65–75% as wide as tall (mean = 71%), and more or less vertical on the posterior face. It is therefore not visible from either the apical or oral surfaces (Pl. 31, figs 1–4). There are no subanal protuberances developed in small individuals, although small protruberances are found on larger individuals (Pl. 32, fig. 2). The periproct opens between interambulacral plates 5 and 10, the lower plates being strongly curved. The periproct lies low on the posterior surface and the distance to the base of the periproct from the lower surface is some 16–25% of the test height (mean = 22%).

Aboral tuberculation consists of small primary tubercles scattered amongst dense miliaries. Larger primary tubercles are found along the inner (interambulacral) margins of the frontal sulcus, where they are approximately three abreast. They are also found close to the apical disc interambulacrally on many juveniles. These adapical tubercles are only slightly larger than other tubercles, but form a characteristic feature where preservation is good. There is no trace of a lateral fasciole. Oral tubercles are slightly larger than adapical ones, but there is no real difference in size between the tubercles of the plastron and those of the latero-ventral regions. The plastron tubercles are largest towards the adambulacral margins and decrease in size towards the midline. Oral ambulacra are smooth and free of tubercles.

REMARKS. I have examined topotype material of this species from Iran and feel secure that the Omani Mountain material is conspecific. However, there is one small difference; the Omani specimens in general have a slightly shallower anterior groove at the ambitus than do the Iranian specimens. This is not considered sufficient to merit separation, since all intermediates can be found. Similarly, *Hemipneustes sardanyolae* Vidal from the late Campanian of Sardanol, Spain, is slightly flatter and more oval in outline, but is otherwise very similar. It too is synonymized here.

The species is readily distinguished from *H. compressus* by its very different, more depressed profile, shallower and very much broader frontal sulcus and central apical disc. It also has better developed phyllodes. It differs from *H. arabicus* in its very broad and shallow frontal sulcus, and from *Opisopneustes* in the lack of aboral primary tubercles.

There is little doubt that the closest species to *H. persicus* is *H. delettrei* (Peron & Gauthier) from the late Campanian of North Africa. Both have a very similar broad, shallow frontal
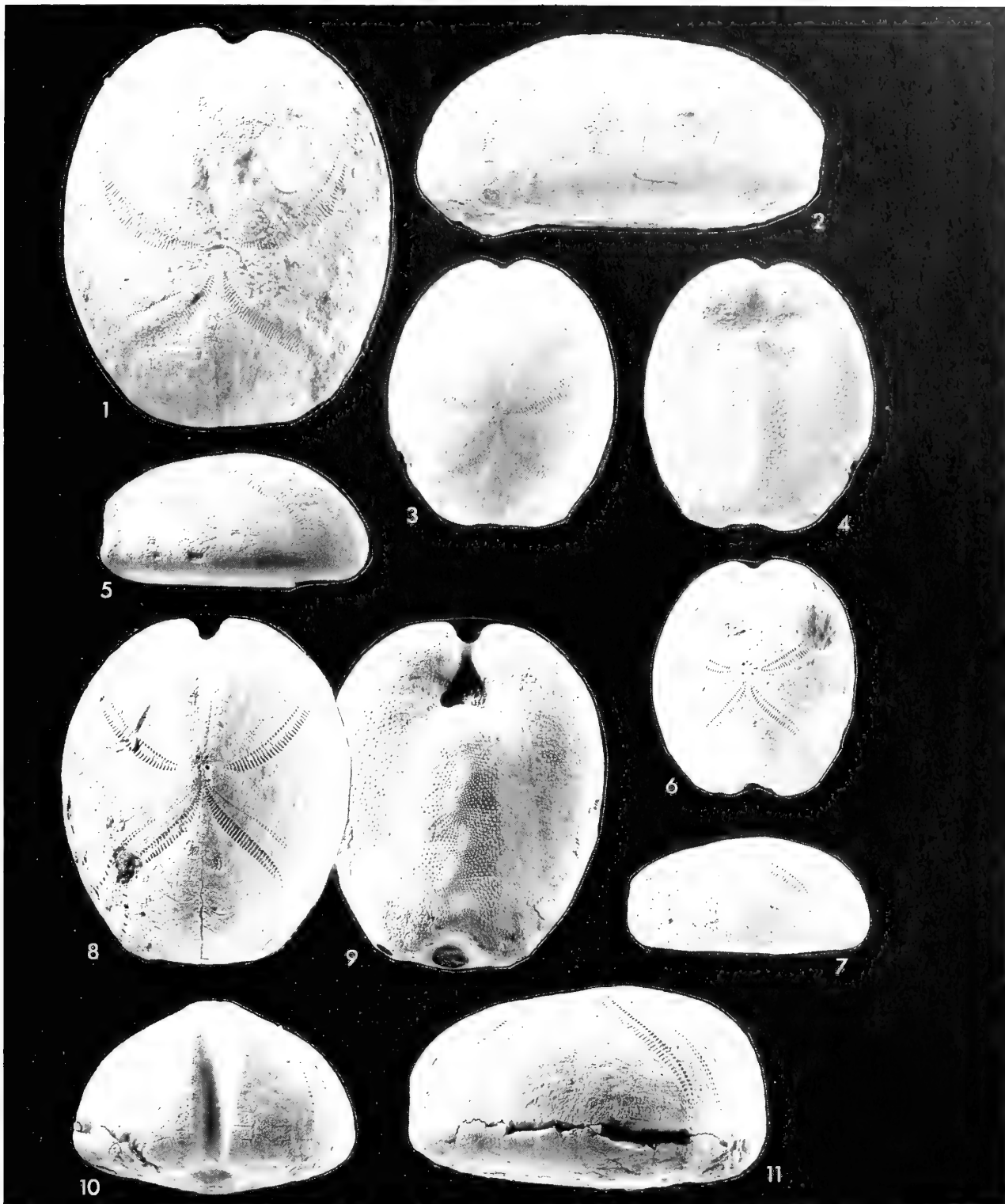
PLATE 31

Figs 1–7 *Hemipneustes persicus* Cotteau & Gauthier. **1, 2,** BMNH EE4084; **1**, apical; **2**, lateral; both × 1. Jebel Rawdah, section 3, bed 5. **3–5,** BMNH EE5032; **3**, apical; **4**, oral; **5**, lateral; all × 1. Jebel Rawdah, section 2, bed 21. **6,** BMNH EE3746, apical, × 1. Jebel Rawdah, section 2, bed 21. **7,** BMNH EE3747, lateral, × 1. Jebel Rawdah, section 2, bed 21.

Figs 8–11 *Hemipneustes compressus* Noetling. BMNH EE3745; **8**, apical; **9**, oral; **10**, anterior; **11**, lateral; all × 1. Jebel Rawdah, section 2, bed 21.

groove that expands continuously towards the anterior, a character seen in no other *Hemipneustes*. *H. persicus* differs from *H. deletrettei* primarily in being very much more depressed in profile and more elongate, with more strongly inflexed petals. However, the differences are not great.

Hemipneustes arabicus Ali, 1989   Pl. 30, figs 1–4; Figs 76, 78B, 80

1989 *Hemipneustes arabicus* Ali: 408, figs 6 (1–3), 7.
1989 *Hemipneustes persicus* Cotteau & Gauthier; Ali: 408, fig. 6 (4).

TYPES. The syntype series are the seven specimens and three fragments mentioned by Ali (1989) as being housed in the Geology Department Museum, Al Ain University, United Arab Emirates. The lectotype, here designated, is his figured specimen (*op. cit.* fig. 6 (1–3)).

MATERIAL STUDIED. Nine specimens: the following description is based on the four best-preserved of these, BMNH EE4085, EE4087–88, EE5027.

OCCURRENCE. This species was first described from Jebel Rawdah, Oman. Specimens were collected from the following horizons at Jebel Rawdah:
Section 1: bed 4 (3).
Section 2: bed 11 (4); bed 14 (1).
Section 4: loose in scree, a little below beds 21/22 (1).

DIAGNOSIS. Test ovate and rather elongate, depressed in side-view and in cross-section arched. Width 76–79% of length, mean = 77%; height 45–46% of length, mean = 45% (size range 76–89 mm). Frontal groove narrow, sharply defined with a small but prominent rim; deeply sunken at the anterior. Apical disc lies at or slightly behind mid-length (distance between anterior and apical disc = 49–55% of test length: mean = 52%). Distinguished from other species by (i) its depressed, elongate profile, (ii) long, sharp and deep anterior groove (iii) central apical disc.

DESCRIPTION. Tests range in length from 77 to 89 mm and in width from 60 to 69 mm (width = 76–79% of length, mean = 77%, SD = 1·1%, N = 4). The widest point lies at or slightly in front of mid-length. In outline the test is oval with a sharp and narrow anterior sulcus and a rather broad posterior truncation (Pl. 30, fig. 1). In side-view the test is depressed and gently rounded (Pl. 30, fig. 4). Test height is 44–46% of length (mean = 45%, SD = 0·8%, N = 4). The tallest point on the test is at, or slightly in front of, the apex. In anterior view the test is uniformly rounded, but there are small crests on either side of the sulcus.

The apical disc is clearly seen in BMNH EE5027 (Fig. 78B). Genital pores are large and separated, with ocular plates II and IV meeting centrally and separating genital plates 2 and 3 from genital plates 1 and 4. Madrepores cover genital plates 2 and 3 and ocular plates II, III and IV. A couple of pores also appear on the margin of genital plate 1. It lies 49–55% of the test length from the anterior border (mean = 52%, SD = 2·5%, N = 4).

Ambulacrum III is narrow and parallel-sided adapically (Pl. 30, fig. 2). It is slightly depressed from the apex until it approaches the anterior border, then it turns rather sharply downwards into a deep groove, 4–6 mm in depth. The sulcus remains narrow throughout, only 11–16% of the test width at the anterior (mean = 13%). Pore-pairs are densely packed
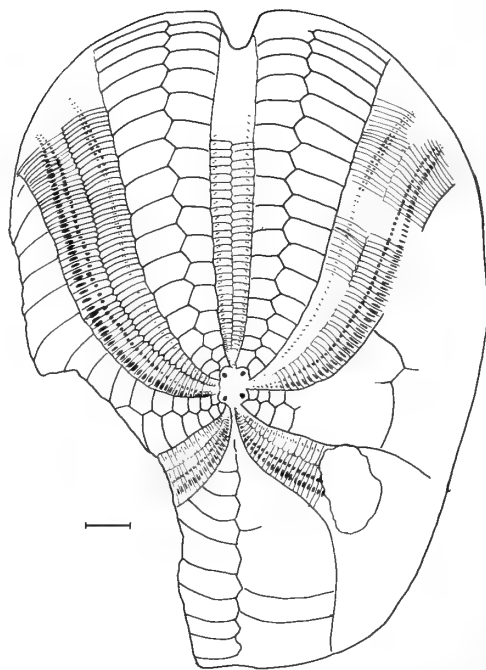
Fig. 80 Camera lucida drawing of adapical plating of *Hemipneustes arabicus*, BMNH EE5027. Scale bar = 5 mm.

along its length until it turns adorally, where they become much more spread out. The floor of the sulcus is covered in fine tuberculation which decreases in size away from the pore-pairs towards the perradius.

The petals are similar in form to those of other species of *Hemipneustes*, the adapical pores in the anterior columns being particularly rudimentary. The anterior petals are flexed forward and diverge at an angle of about 15° to the frontal groove before curving laterally near their distal end (Fig. 80). The posterior petals diverge at about 110–120° to each other. Adorally there are well-developed phyllodes, with five or six pores in a column in the lateral ambulacra.

The plastron consists of a small, broad labral plate and a series of four or five wedge-shaped plates that extend across the full width of the plastron (Fig. 80). Posterior plates are biserial. The peristome is oval, indented slightly by the labral plate, and predominantly forward-facing. It lies at the base of the anterior sulcus, some 16% of the test length from the anterior border.

The periproct is oval and downward facing; clearly visible from below but hidden from above (Pl. 30, figs 1, 2). The test is developed into two prominent bulges, one on either side of the periproct. The periproct lies between interambulacral plates 5 and 10. The base of the periproct lies between 19 and 26% of the test height above the base.

Tuberculation is fine and uniform over the apical surface, except along the inner interambulacral margins of the frontal groove, where larger primary tubercles are developed. Oral tuberculation is slightly coarser, with ambulacral zones free of any tuberculation. No lateral fasciole is seen.

REMARKS. This species appears somewhat intermediate between the broad grooved *H. persicus* and the tall, narrow-grooved but upright *H. compressus*. It differs from *H. persicus* in the sharpness and narrowness of its anterior
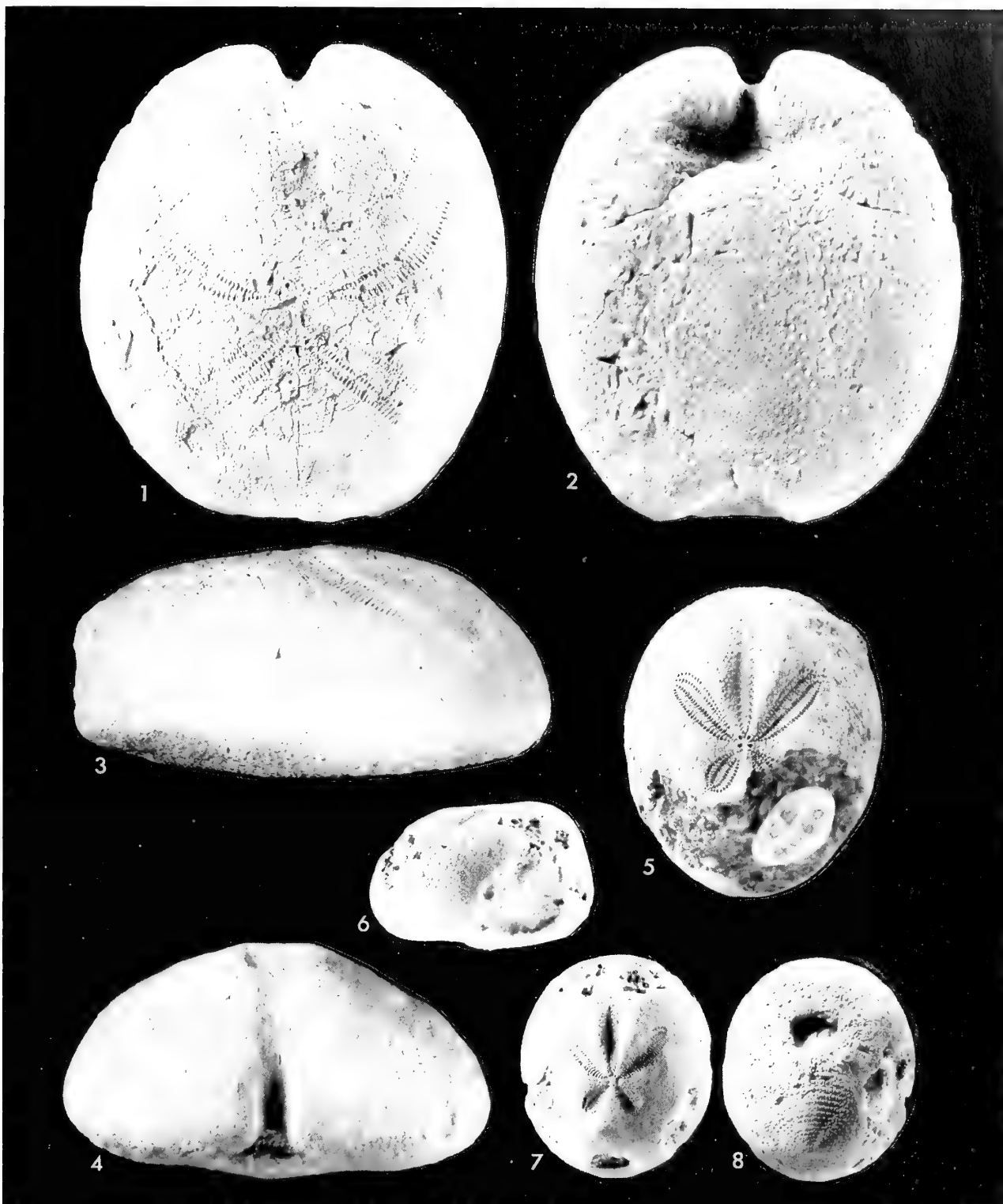
PLATE 32

Figs 1–4 *Hemipneustes persicus* Cotteau & Gauthier. Specimen in the Morgan Collection, Museum d'Histoire Naturelle, Paris; **1**, apical; **2**, oral; **3**, lateral; **4**, anterior; all × 2. Arkouraj, Iran.

Figs 5–8 *Hemiaster hattaensis* Ali. **5**, BMNH EE4060; apical, × 2. Jebel Thanais, basal 2 m of the Simsima Formation. **6–8**, BMNH EE4059; **6**, lateral; **7**, apical; **8**, oral; all × 1·5. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation.

sulcus. In *H. persicus* the frontal groove is much broader and lacks the interambulacral keels. It is also much less deeply indented at the ambitus. However, like *H. persicus*, *H. arabicus* has its apical disc at or slightly behind mid-length, in contrast to *H. pyrenaicus* where the test is more quadrate and the apical disc lies anterior of centre. Like *H. compressus*, *H. arabicus* shows a sharp change from apical to anterior sectors of its anterior sulcus.

Order **SPATANGOIDA** Claus, 1876
Family **HEMIASTERIDAE** Clark, 1917
Genus *HEMIASTER* Agassiz, in Agassiz & Desor, 1847

***Hemiaster hattaensis* Ali, 1989**   Pl. 32, figs 5–8; Figs 81C–E

?1903   *Hemiaster* sp. Lambert: 87, pl. 3, figs 6–8.
1989   *Hemiaster (Bolbaster) hattaensis* Ali: 409, fig. 6 (5–8).

TYPES. Eleven specimens referred to by Ali form the syntype series since no holotype was designated. These are in the Geology Department Museum, University of Al Ain, United Arab Emirates.

MATERIAL STUDIED. Thirteen specimens, of which the following six were used for the biometric study: BMNH EE4055, EE4057, EE4059–60, EE4064 and EE4320.

OCCURRENCE. The species is known for certain only from the western Oman mountain. It has been found at the following localities:
Jebel Buhays, section 1: loose in the scree, derived from the lowest few metres of the Simsima Formation (5).
Jebel Thanais: lowest 2 metres of the Simsima Formation (1).
Jebel Rawdah, section 1: bed 6 (3).
Jebel Rawdah, section 2: loose in scree (1).
Jebel Rawdah, section 3: bed 5 (1).
Jebel Rawdah, section 4: bed 2 (1); bed 13 (1).

DIAGNOSIS. An ovate *Hemiaster* with cruciform petals in which the posterior pair are about half the length of the anterior pair. Apical disc ethmophract, with the posterior genital plates L-shaped and separating the posterior ocular plates; lying posterior to midlength. Ambulacrum III long, narrow, depressed adapically but becoming flush with surrounding area towards the ambitus.

DESCRIPTION. Tests oviform with a uniformly rounded anterior and a slightly pointed posterior (Pl. 32, fig. 5). Test length is 15–32 mm and test width 11–26 mm (width = 82–87% of length in larger individuals but only 75% in a juvenile 15 mm long). The widest point lies about mid-length. Test rather depressed in profile (Pl. 32, fig. 6), with a height 55–67% of length (mean = 64%, SD = 4·6%, N = 6). Lower surface gently convex with a slight keel to the plastron towards the peristome. Upper surface flat towards the posterior, sloping uniformly towards the anterior (Pl. 32, fig. 6). The tallest point on the test lies just posterior to the apical disc.

The apical disc is ethmophract (Fig. 81D) and lies 58–62% of the test length from the anterior border in adults, but further (73%) in the juvenile 15 mm in length. Anterior gonopores are set closer together than the posterior pair. Genital plates 2 and 3 are relatively small whereas genital plates 1 and 4 are longer and L-shaped and are broadly in contact (Fig. 81D). There are relatively few madrepores developed. Ocular plates are small, pentagonal and project.

The anterior ambulacrum is sunken adapically but the sulcus is lost about two-thirds of the way towards the ambitus and there is no indentation at the ambitus (Pl. 32, figs 5, 7). The adapical sulcus is parallel-sided and very narrow. There are 14 pore-pairs in a column in 17–18 mm individuals and these are strongly oblique with a prominent interporal partition. The floor of the sulcus is covered in fine and dense granulation. Pores beyond the peripetalous fasciole are single and minute. The interambulacra on either side of the frontal sulcus are keeled, especially in the larger specimens.
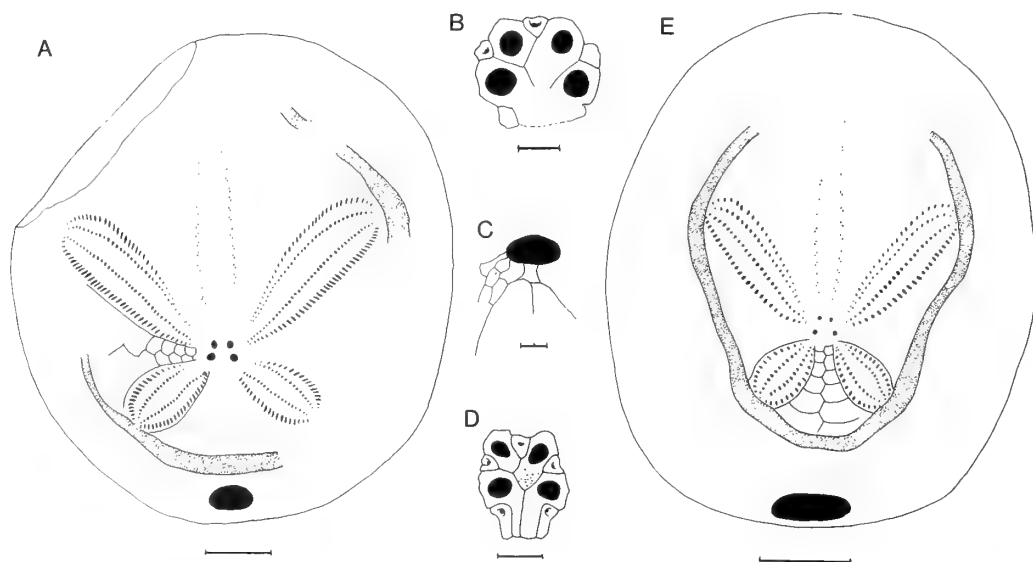
Fig. 81   Camera lucida drawings of plating in *Hemiaster* species. **A, B**, *Hemiaster paronai* Checchia-Rispoli, BMNH EE5034: A, apical surface (fasciole stippled); B, apical disc. **C-E**, *Hemiaster hattaensis* Ali: C, peristome and labral plate, BMNH EE4064; D, apical disc, BMNH EE4060; E, apical surface (fasciole stippled), BMNH EE4059. Scale bars: A, E = 5 mm; B, D = 1 mm; C = 2 mm.

The petals are cruciform and sunken, the anterior pair being twice as long as the posterior pair (Pl. 32, figs 5, 7; Fig. 81E). Pore-pairs are broad and conjugate and the columns close distally. The perradial zone is slightly narrower than the pore-pair zones on either side. There are 12–14 pore-pairs in a column in the posterior petals and 24–26 in the anterior petals in individuals 15–18 mm in length.

The periproct is tear-drop shaped, pointed adapically, and lies high on the posterior face. It is about 3 mm wide and 4 mm in height in an individual 17 mm in length. The base of the periproct lies 55–58% of test height above the base.

The peristome is D-shaped and is 1·6 to 1·8 times as broad as wide. It lies 24–29% of the test length from the anterior border in 17–18 mm length individuals. It is neither invaginated nor does it have a surrounding rim, as is seen in many *Hemiaster* species. The plastron is broad, with a straight, median suture (Fig. 81C). It is covered in dense orderly rows of tubercles. The labral plate is vase-shaped and relatively small. Surrounding the peristome there are four phyllode pores in each column of a lateral ambulacrum and three in the posterior ambulacrum. There are also two or three enlarged subanal pore-pairs.

There is a well-developed peripetalous fasciole that is without sharp angles. The remainder of the upper surface has scattered primary tubercles and dense miliaries.

REMARKS. Ali (1989) erected this species for 11 specimens from Jebel Rawdah. It resembles *H. aquisigranensis* Schlüter in the form of its petals and frontal groove, but differs from that species in having a larger peristome and having a vertical or slightly outward-sloping posterior. In *H. aquisigranensis* the posterior is strongly retrenched, such that the periproct is visible from the oral surface rather than the aboral surface. *H. hattopsis* undoubtedly comes closest to *H. punctatus* d'Orbigny, from the late Campanian of France. However, this species differs in being very much smaller, more elevated and in having a well developed rim to the peristome.

Lambert (1903) described and figured a badly preserved specimen that may be conspecific. Lambert's specimen came from the late Cretaceous of Fanivelona, eastern Madagascar. It has a very similar overall shape, but unfortunately the apex of the test is damaged and only the anterior petal on one side is preserved. It is only tentatively assigned to this species.

Hemiaster paronai Checchia-Rispoli, 1921   Pl. 33, figs 1–4; Figs 81A, B

1921   *Hemiaster Paronai* Checchia-Rispoli: 27, pl. 8, fig. 24, pl. 9, figs 14–18.
1932   *Hemiaster Paronai* Checchia-Rispoli; Checchia-Rispoli: 8, pl. 2, figs 1–8.
?1967   *Hemiaster punctatus* d'Orbigny; Devries: 194, pl. 6, figs 34–41.
?1967   *Hemiaster regulusanus* d'Orbigny; Devries: 194, pl. 6, figs 42–44.

MATERIAL. Seven specimens, only one of which is well-preserved, BMNH EE5034.

OCCURRENCE. Specimens were found at the following localities and horizons in the western Oman mountains:
Jebel Huwayyah, section 1: bed 9 (1); bed 11 (1).
Jebel Huwayyah, section 2: beds 3–5 (3).
Jebel Faiyah, section 1: bed 4 (1).
Jebel Rawdah, section 3: bed 9 (1).

Elsewhere the species has been recorded from the Maastrichtian of northern Libya.

DIAGNOSIS. Like *H. hattaensis* but more inflated and more circular in outline, with deeper petals and deeper and wider anterior sulcus adapically.

DESCRIPTION. The best preserved specimen is 37·1 mm in length, 35·6 mm in width (96% of length: widest point approximately mid-length) and 28·8 mm in height (78% of length). In outline the test is more or less circular and in profile the upper and lower surfaces are broad and flat with the anterior uniformly rounded and the posterior sloping steeply outwards (Pl. 33, figs 1–4).

The apical disc is ethmophract with the posterior two genital plates rather stout and broadly in contact (Fig. 81B). The posterior ocular plates are separated. Gonopores are large and occupy most of the plate, but in some individuals (?males) may be relatively smaller. Genital plate 2 has a small central zone of madrepores. The apical disc lies 58% of the test length from the anterior border.

The anterior ambulacrum lies in a frontal sulcus which is bordered by sharp interambulacral crests adapically but which shallows and is lost towards the ambitus (Pl. 33, fig. 2). There are 22 pore-pairs in a column between the apex and the peripetalous fasciole and these are strongly oblique. The sulcus is rather narrow and slightly lanceolate in outline.

The petals are cruciform with the anterior pair twice the length of the posterior pair (Fig. 81A). There are 40 pore-pairs in a column in the anterior pair and 21 in the posterior pair at 37 mm test length. Petals close distally and the perradial interporal zone is narrower than either of the bordering pore zones.

The periproct is oval, slightly pointed adapically and lies high on the posterior side. It is just visible from above because of the outward slope of the posterior face. It is about 70% as wide as tall and is 18% of the test height in height. Its base lies 60% of test height above the base (Pl. 33, fig. 4).

The peristome is D-shaped, twice as wide as long and lies 28% of the test length from the anterior border. It is not rimmed. There are five phyllode pores in each column of lateral and posterior ambulacra. There are also five subanal pore-pairs in the two posterior interambulacra.

REMARKS. This species closely resembles *H. hattaensis* in the shape of petals, apical disc structure and the form of the anterior ambulacrum. However, it differs consistently in shape, being both more rounded in outline and more inflated in profile. This is not simply an attribute of size, since the small specimens from Jebel Huwayyah (eg. BMNH EE4061, 22 mm in length) are very different in shape from similar-sized individuals from Jebel Buhays. In addition the pore-pairs in the frontal groove are more numerous and more densely packed.

The specimens appear indistinguishable from those described from the Maastrichtian of Libya by Checchia-Rispoli (1921) under the name *H. paronai*. Very similar material was also described by Devries (1967) from the Maastrichtian of Turkey under the names *Hemiaster punctatus* d'Orbigny and *H. regulusanus* d'Orbigny. Unlike the specimens described here and by Devries (1967), *H. punctatus* has a large flush peristome lacking a rim. The species is also very similar to *Hemiaster noemiae* Cotteau & Gauthier, from the late Senonian of southern Iran (Pl. 33, figs 5–8). However, *H. noemiae* differs in having a shorter anterior
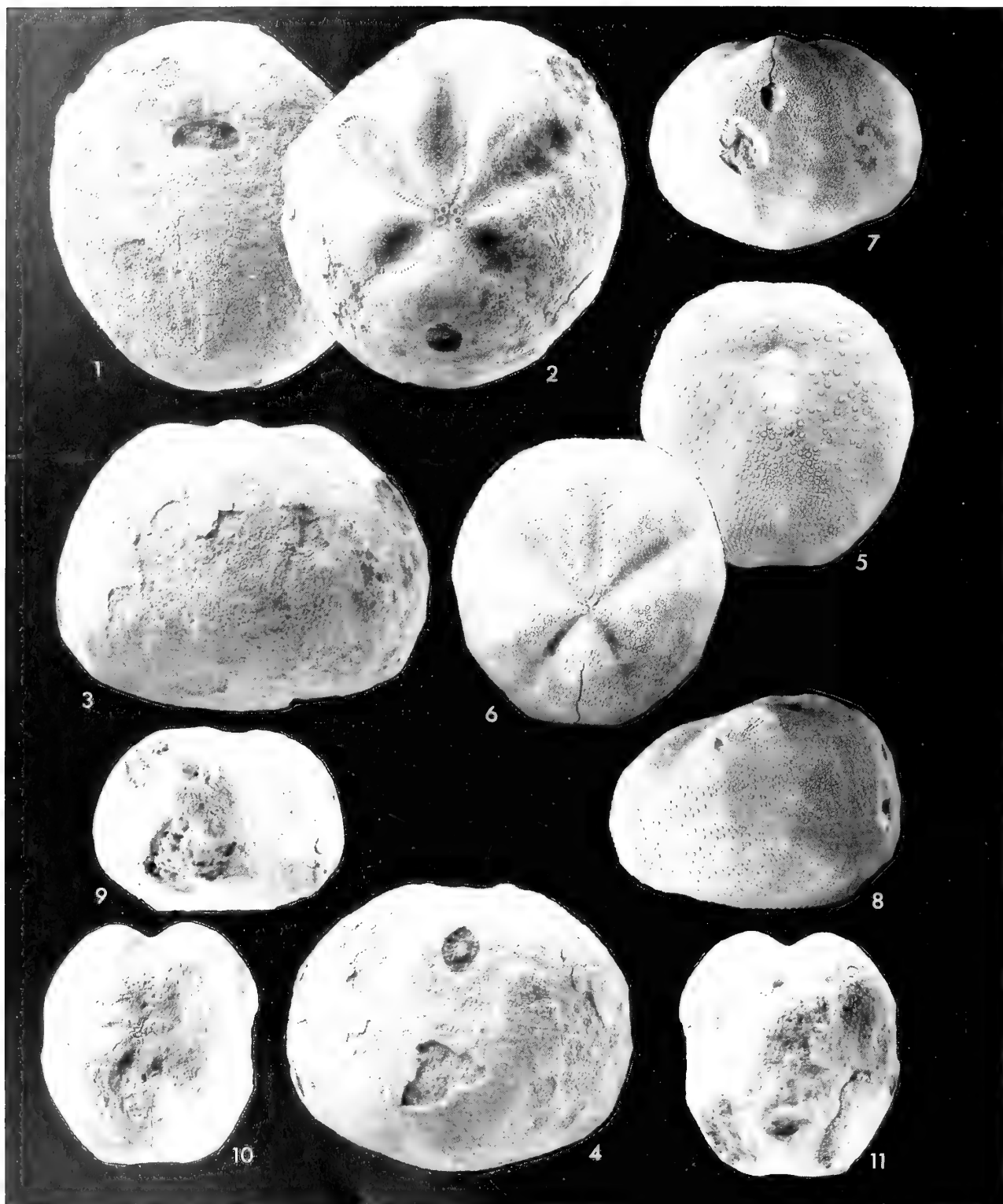
PLATE 33

Figs 1–4   *Hemiaster paronai* Checchia-Rispoli. BMNH EE5034; **1**, oral; **2**, apical; **3**, lateral; **4**, posterior; all × 2. Jebel Rawdah, section 3, bed 9.

Figs 5–8   *Hemiaster noemiae* Cotteau & Gauthier. B18727, Morgan Collection, Museum d'Histoire Naturelle, Paris; **5**, oral; **6**, apical; **7**, posterior; **8**, lateral; all × 2. Senonian of Awasa, Iran.

Figs 9–11   ?*Linthia sudanensis* (Bather). BMNH EE4054; **9**, lateral; **10**, apical; **11**, oral; all × 1·5. Loose near top of section at Jebel Rawdah, section 3.
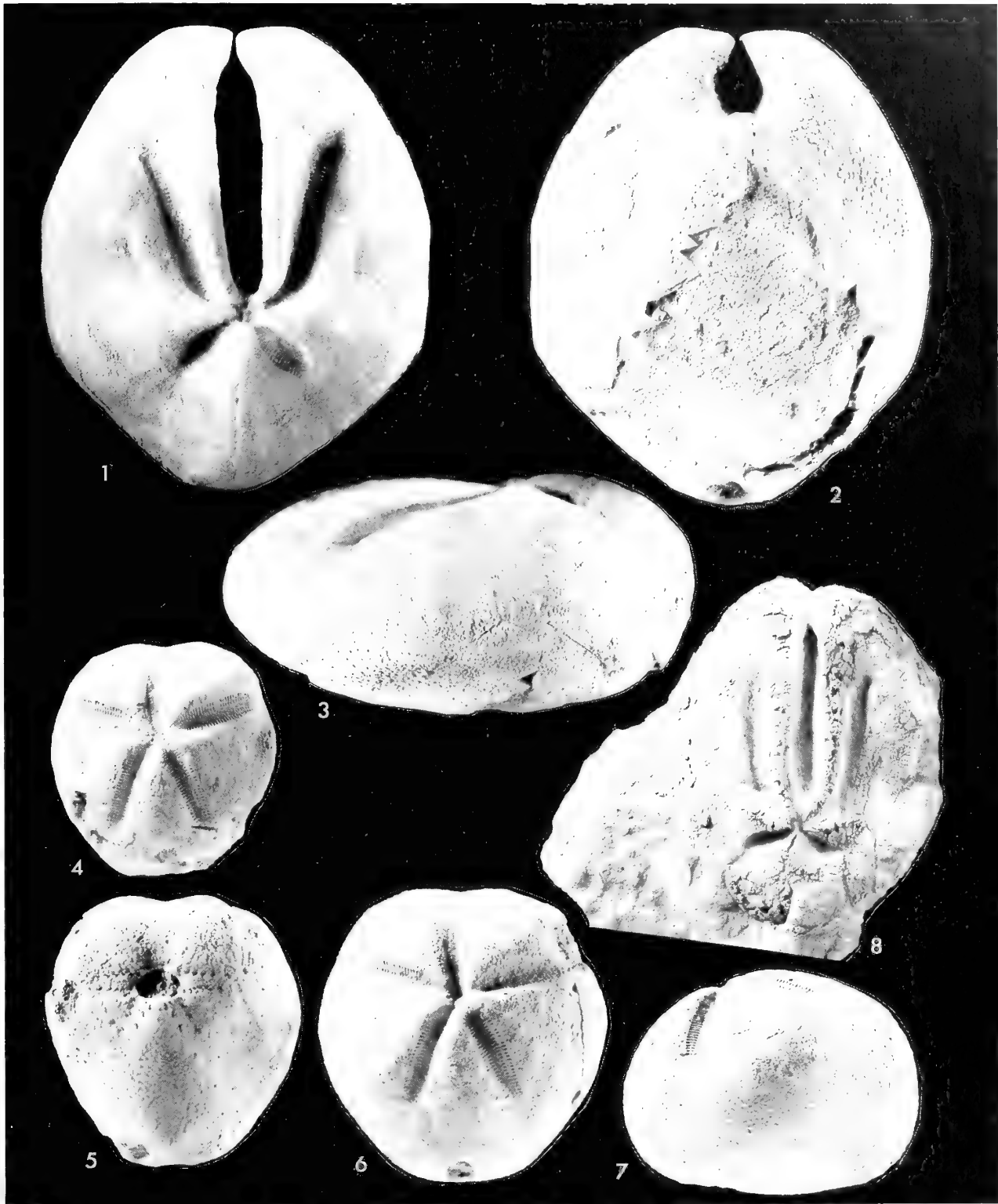
PLATE 34

Figs 1–3, 8 *Proraster geayi* Cottreau. **1–3**, specimen in Museum d'Histoire Naturelle, Paris; **1**, apical; **2**, oral; **3**, lateral; all × 2. Maastrichtian of Antanihody, Madagascar. **8**, BMNH EE4067, apical, × 1. Jebel Huwayyah, section 1, bed 18.

Figs 4–7 *Mecaster victoris* (Lambert). Jebel Rawdah, section 3, bed 5. **4**, BMNH EE4050; apical, × 2. **5**, BMNH EE4049; oral, × 2. **6, 7**, BMNH EE4042; **6**, apical; **7**, lateral; both × 2.

sulcus with many fewer pore-pairs, and in having a much smaller peristome at comparable sizes.

Genus *MECASTER* Pomel, 1883

Mecaster victoris (Lambert, 1932) Pl. 34, figs 4–7; Figs 82–84A

1932   *Hemiaster Victoris* Lambert: 127, pl. 4, figs 18, 19.
1967   *Hemiaster* sp. Devries: 194, pl. 6, figs 45–47.
1990   *Periaster subsexangulatus* Airaghi; Ali: 410, fig. 5 (8).

MATERIAL STUDIED. Ten reasonably complete specimens were used in the biometric analysis, BMNH EE4035–36, EE4038–40, EE4042, EE4045–46, EE5035–36. Another 32 specimens were collected.

OCCURRENCE. In the study area, this species was found at the following localities and horizons:
Jebel Buhays, section 1: loose in the scree, derived from the lowest few metres of the Simsima Formation (1).
Jebel Huwayyah, section 1: bed 14 (1).
Jebel Huwayyah, section 2: beds 3–5 (3).
Jebel Rawdah, section 3 (top of bed 5 (28): bed 8 (2); beds 9/10 (7).

The species was originally described from the Campanian of El Kantara, Algeria. A poorly preserved specimen that also appears identical was described from the Maastrichtian of Cortinek, Turkey.

DESCRIPTION. Specimens range in size from 24 to 33 mm in length. Mean test width is 98% of the length (range 93–100%, SD = 3·2%, N = 9) and test height 76% of the length (range 72–80%, SD = 3·1%, N = 7). The test is weakly cordiform in outline, tapering posteriorly to a rounded point and with the widest point in front of the mid-line (Pl. 34, figs 4–6). In profile the test is inflated with a rounded posterior and anterior (Pl. 34, fig. 7). The tallest point is posterior of the apical disc.

The apical disc lies 36–40% of the test length from the anterior border (mean = 38%, SD = 1·4%, N = 8). It is ethmolytic with the posterior oculars separated by the madreporite (Fig. 84A). The gonopores on each side of the mid-line lie close together.

Although ambulacra are sunken, they are all rather shallow and relatively narrow (Pl. 34, figs 4, 6; Fig. 83A). Pore-pairs in the anteal sulcus are small and situated along the adradial margins. The anterior petals are long, narrow and straight-sided. They extend most of the way to the ambitus and diverge from one another at an angle of 130°. There are 33 pore-pairs in a column at 25 mm test length, rising to 36 at 29 mm test length. The pore-pairs are narrow, with the outer pore in each pair slightly more elongate than the inner. The posterior petals extend about 75% of the distance to the ambitus and are equally narrow and parallel-sided. They are about 85-90% of the length of the anterior petals and have 28 pore-pairs in a column at a test diameter of 25 mm, rising to about 32 at 28 mm.

The periproct is high on the posterior and is usually just visible from above. The base lies more or less half way up the posterior face (mean = 50%, SD = 4·5%, N = 4). The opening is vertically elongate, being about 1·6–1·8 times as tall as broad, and is pointed adapically.

The peristome is D-shaped and lies about 20% of the test length back from the anterior border (range 18·5–21·5%, SD = 1·1%, N = 6). The labrum projects slightly over the opening. The labral plate is relatively long and narrow, almost parallel-sided (Fig. 83B). It meets only one of the sternal plates.

Tuberculation is fine adapically, slightly coarser adorally. There is always a peripetalous fasciole, some 0·6 mm in width. Although preservation is usually too poor to allow its course to be traced fully, there appears to be little indentation of the peripetalous fasciole laterally and it runs close to the ambitus. In one specimen (BMNH EE4050) there is a distinct latero-anal fasciole also, but other specimens, equally well preserved in this region have only rudimentary traces of such a fasciole or no fasciole at all. It is clear that the latero-anal fasciole is variably developed in this species.

REMARKS. Lambert (1932: 127) created this species on the basis of material from the late Campanian of El Kantara, Tunisia. It has narrower, shallower petals than other *Mecaster* species and in profile is inflated with the tallest point lying well to the posterior. Lambert noted that there were traces of a latero-anal fasciole in six out of twelve specimens, while another three had a distinct latero-anal fasciole. Lambert separated those with a latero-anal fasciole and placed them in his '*Periaster Victoris*', though recognising that they were completely intergradational with *Hemiaster victoris*. As Lambert quite correctly pointed out, the presence/absence of a latero-anal fasciole is highly variable and the various species classified under the genus *Periaster* are polyphyletic in origin.

Ali (1989) figured a specimen of this species without description under the name *Periaster subsexangulatus* Airaghi. However, *P. subsexangulatus* has a much broader, deeper anteal sulcus, is less rounded and less inflated and most particularly, the petals are broader and less parallel-sided and the posterior pair are distinctly shorter than the anterior pair.

The plastron structure is significant in that the labral plate is in contact with sternal plate 2b only (Fig. 83B). This is also the situation in *Iraniaster* and other Somaliasteridae. *Iraniaster* has been placed in the Holasteroida on account of its plastron structure, yet it has a compact apical disc in which the posterior genital plates, but not the posterior ocular plates, are separated by the madreporite (Kier 1972, figs 41–42). The fact that a meridoplacous plastron can be developed in at least one *Mecaster* species, and the similarity of apical disc plating strongly indicates that somaliasterids are derived from the *Mecaster* lineage.

Family **SCHIZASTERIDAE** Lambert, 1905
Genus **LINTHIA** Desor, 1853

?Linthia sudanensis (Bather, 1904) Pl. 33, figs 9–11; Figs 84B, 85

?1904   *Hemiaster sudanensis* Bather: 299, pl. 11, figs 6–13.

MATERIAL. One specimen, BMNH EE4054.

OCCURRENCE. The specimen was found loose about 8 m below the top of section 3 at Jebel Rawdah, western Oman. The section here is capped by a two metre thick conglomerate of reworked Simsima Limestone and thus the specimen could be of late Maastrichtian age.
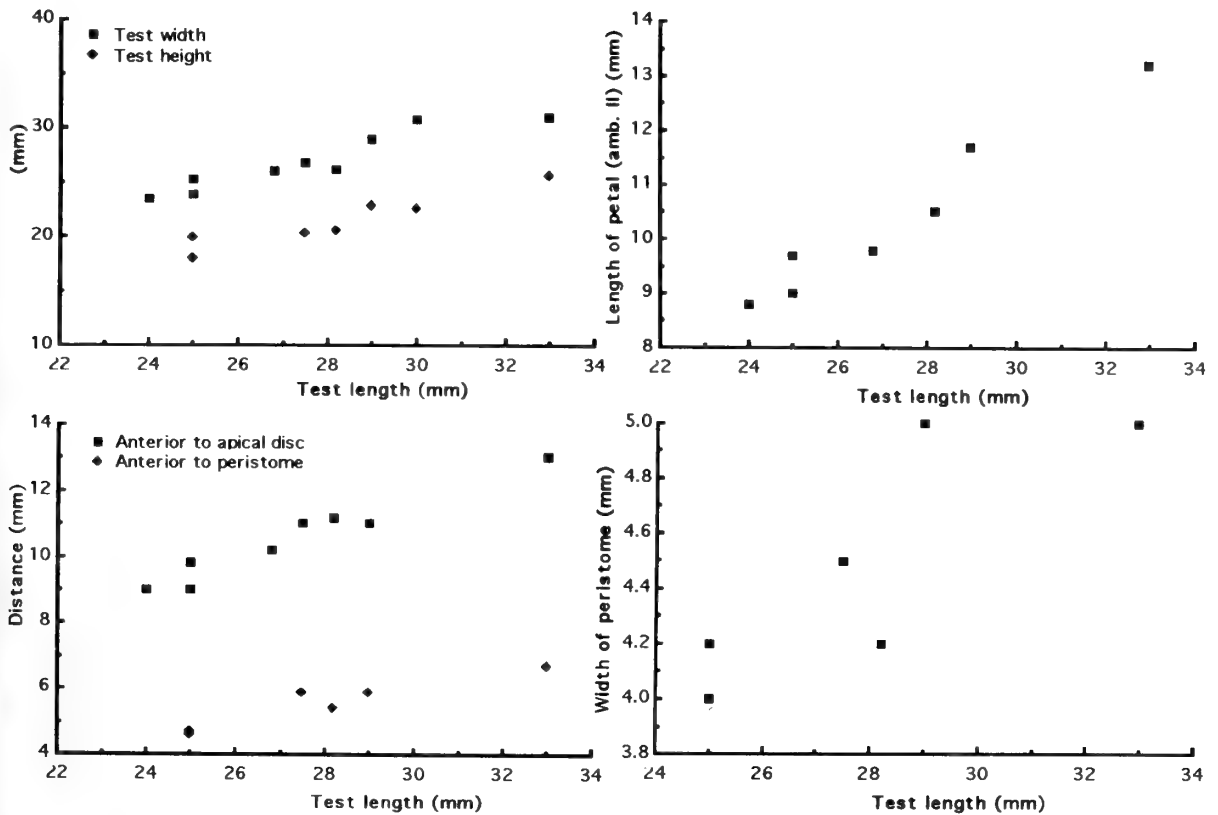
Fig. 82 Biometric data for *Mecaster victoris* (Lambert).
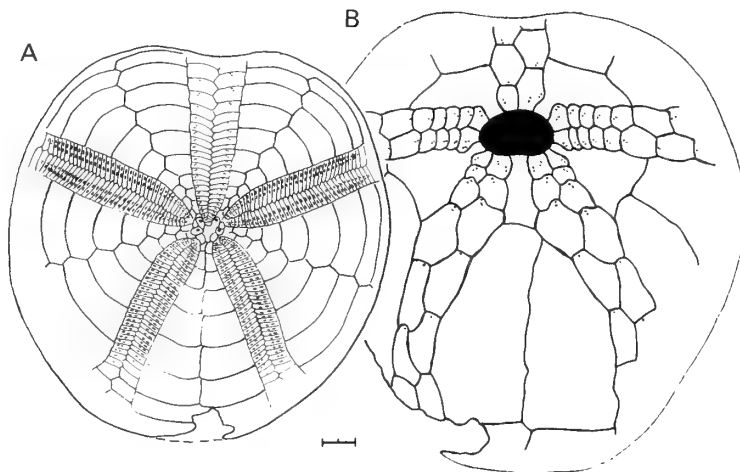
Fig. 83 Camera lucida drawings of plating in *Mecaster victoris* (Lambert). **A**, apical surface, BMNH EE4050; **B**, oral surface, BMNH EE4049. Scale bar = 2 mm.

DESCRIPTION. The specimen is not well preserved but retains sufficient features to be able to place it generically. The test is 32·5 mm in length, 30·5 mm in width (93% of length) and 24 mm in height (74% of length). It is heart-shaped in outline with a squarely truncated posterior and a rather deep anteal sulcus, approximately 2·5 mm deep (7% of test length). The anteal sulcus is relatively broad and deepens gradually away from the apex. In profile the test is rather flat above and below and has a rounded anterior and steep posterior.

The apical disc is ethmolytic and gonopores are large, those on either side almost touching (Fig. 84B). It lies well anterior of the centre, the anterior gonopores being 38% of the test length from the anterior border. The posterior ocular plates are separated by the posteriorly elongated madreporite plate. The antero-lateral ocular plates project and hardly indent the adjacent genital plates.

The anterior sulcus has small isopores that are not crowded together. The anterior petals are 13·5 mm in length and
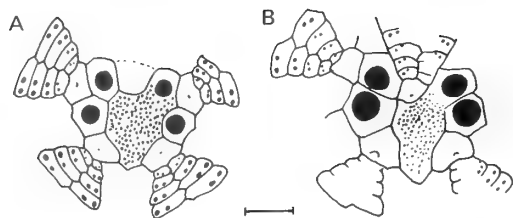
Fig. 84 Camera lucida drawing of apical discs. **A,** *Mecaster victoris* (Lambert), BMNH EE4050. **B,** *?Linthia sudanensis* (Bather), BMNH EE4054. Scale bar = 1 mm.
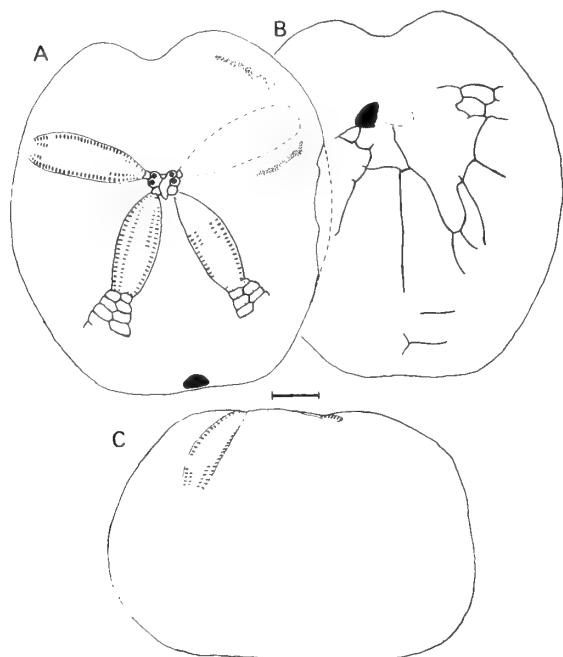
Fig. 85 Camera lucida drawing of *?Linthia sudanensis* (Bather), BMNH EE4054. **A,** apical; **B,** oral; **C,** lateral. Scale bar = 5 mm.

widely divergent (Fig. 85). They extend for most of the distance to the ambitus when viewed from above. Inner and outer pores are equally slit-like and there are 33 pore-pairs in a column. The posterior petals are shorter, only 10 mm in length, and reach approximately half-way towards the ambitus. There are 24 pore-pairs in a column.

The periproct is just visible from above. It is 6·5 mm in height and 4 mm in width, being pointed adapically. The base of the periproct lies just above mid-height, some 11·3 mm above the base of the test (52% of test height).

The plastron is asymmetric, with the median suture displaced towards the right. The labral plate is short (11·5 of the test length) and trapezoidal in outline. The peristome is D-shaped although the labral plate does not project over the peristome much. The peristome is set rather far back from the anterior border, its anterior margin being 23% of the test length from the anterior.

REMARKS. The specimen is unfortunately very badly preserved and cannot be identified to species level with any certainty. However, from the general shape and petal form it cannot be distinguished from the common Palaeocene species *Linthia sudanensis* described by Bather (1904) from Sudan.

Genus *PRORASTER* Lambert, 1895

Proraster geayi Cottreau, 1908   Pl. 34, figs 1–3, 8

1908   *Proraster Geayi* Cottreau: 26, pl. 4, fig. 5.

TYPES. The syntypes of *P. geayi* are the two specimens described from Marohita, eastern Madagascar by Cottreau (1908) stated to be in the Museum d'Histoire Naturelle, Paris.

MATERIAL STUDIED. Six specimens, BMNH EE4065–69, EE5037, none of which are particularly well-preserved.

OCCURRENCE. In the western Oman Mountains this species occurs as juveniles in beds 3–5 at Jebel Huwayyah, section 2 (2). Large individuals occur in bed 18 at the top of section 1, Jebel Huwayyah (7), and in bed 9 at Jebel Rawdah, section 1 (2). It is also found in the Maastrichtian of Madagascar.

DIAGNOSIS. A *Proraster* with a very deep anteal sulcus that is closed or almost closed distally by convergence of the lateral walls.

DESCRIPTION. No test is well-preserved, the best specimens being BMNH EE4067 and EE4068. The former is a large individual 71 mm in length, 56 mm in width and about 27 mm in height, whereas the latter is a much smaller individual 27 mm in length, 24 mm in width and 15·6 mm in height. The test is oval in outline with its widest point slightly posterior of midline (Pl. 34, fig. 8). In profile the test is depressed and wedge-shaped, sloping gradually towards the anterior. The posterior is almost vertical and the tallest point on the test lies close to the posterior.

The apical disc lies well towards the posterior, 66–69% of test length from the anterior border. Plating is not seen in any specimen.

The anterior ambulacrum is extremely deep and at the ambitus is about 10% of the test length in depth. The walls are concave with the adjacent interambulacra curving over the groove. Towards the anterior the two sides almost touch so as to roof over the sulcus. The groove thus appears pinched shut close to the anterior (Pl. 34, figs 1, 8).

Petals are sunken. The anterior pair curve forward and run parallel with the anteal sulcus for about two thirds of its length. The posterior petals are very much shorter (about one third of the length of the anterior petals) and diverge strongly at about 120°. There is a well developed peripetalous fasciole developed at the base of the petals, which is presumably continuous, but is not seen other than in small patches because of poor preservation. There is no evidence of a latero-anal fasciole.

The peristome is positioned far forward, lying at the base of the anteal sulcus, and faces anteriorly. The periproct is large and situated high on the posterior face.

REMARKS. Although the Omani specimens to hand are not well-preserved they show sufficient detail to be unambiguously assigned to this species. *P. geayi* was first erected for large individuals from the Maastrichtian of Madagascar by Lambert (1908). Lambert (1905) had previously erected the genus *Proraster* for *Schizaster atavus* (Arnaud) from the Campanian of Charante, France and two Iranian species *Opissaster morgani* (wrongly cited as *O. Douvillei*) and *O. centrosus* Cotteau & Gauthier (1895). The genus was erected to encompass *Schizaster*-like forms lacking a latero-anal fasciole.

The species of Cotteau & Gauthier are unfortunately based

on small individuals and are thus not directly comparable with *P. geayi*. Differences between *P. morgani* and *P. centrosus* seem slight and restudy may prove them synonymous. Because they are small, there is the possibility that they represent juveniles of *P. geayi*. However, this seems unlikely since they have much wider and less pinched anterior sulci than very slightly larger individuals of *P. geayi* found in the lower beds at Jebel Huwayyah. This pinching of the frontal groove, whereby the two sides converge and almost touch near the anterior border, becomes very much more pronounced in the larger individuals higher in the section. This character serves to distinguish *P. geayi* from both *P. atavus*, and an undescribed ?Campanian species from Nafun, Oman. Cotteau & Gauthier's species also have a much less well developed anterior notch and their peristome is standard in orientation rather than being subvertical and directed towards the anterior.

It is noteworthy that at Jebel Huwayyah only small individuals are found in the lower levels, in the *Loftusia* facies, while large individuals are found near the top of the section in carbonate marls representing shelf basinal facies. This could be because the two samples represent different species with consistent morphological differences, or because the smaller individuals are juveniles of the larger, but inhabit a different biotope. Without considerably more and better preserved material it is impossible to determine which is correct. For the present I treat the two forms as juveniles and adults of the same species, partially because the small forms are much closer in appearance to the large forms than they are to, for example, *P. morgani*.

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Maastrichtian ammonites from the United Arab Emirates-Oman border region

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INTRODUCTION

The ammonites described are from the late Cretaceous Qahlah and Simsima Formations of the United Arab Emirates-Oman border region and come from two collections. Some of the specimens were collected by Dr. P.W. Skelton (Open University) in 1990 and are housed in Oxford University Museum (OUM prefixes). The remainder are housed in the Natural History Museum, London (BMNH prefixes) and were mostly collected by A.B. Smith and N.J. Morris during fieldwork in 1991 and 1992. A few specimens were collected by amateur enthusiasts and subsequently donated to the Natural History Museum.

Wherever possible, ammonites have been tied down to specific levels within measured sections. Details of the localities of these sections, and measured lithological logs are given in a preceding section (Smith *et al.*).

SYSTEMATIC DESCRIPTIONS

Order **AMMONOIDEA** Zittel, 1884
Suborder **AMMONITINA** Hyatt, 1889
Superfamily **DESMOCERATACEAE** Zittel, 1895
Family **DESMOCERATIDAE** Zittel, 1895
Subfamily **DESMOCERATINAE** Zittel, 1895
Genus *DESMOPHYLLITES* Spath, 1929

(= *Schlüteria* de Grossouvre, 1894: 126 (*non* Fritsch *in* Fritsch & Kafka, 1887: 33); *Schlütericeras* Collignon, 1938: 92 (*non* Hyatt, 1903: 110))

TYPE SPECIES. *Desmoceras larteti* Seunes, 1892: 19, pl. 12 (3), fig. 2; pl. 13 (4), figs 2, 3, by subsequent designation by Spath 1921: 46, as type species of *Schlüteria* de Grossourvre, of which *Desmophyllites* is the replacement name.

Desmophyllites diphylloides (Forbes, 1846)   Plate 1, figs 1, 2

1846   *Ammonites diphylloides* Forbes: 105, pl. 8, fig. 8.
1992   *Desmophyllites diphylloides* (Forbes); Kennedy & Henderson: 405, pl. 6, figs 1–9; pl. 16, figs 1–3, 7–8; pl. 17, figs 4–7; fig. 3F (with full synonymy).
1993a *Desmophyllites diphylloides* (Forbes); Kennedy & Cobban: 120, pl. 1, figs 1–8; text-fig. 5c.

TYPES. Lectotype, by the subsequent designation of Matsu-

moto & Obata (1955: 122) is BMNH C22682, the original of Forbes 1846: pl. 8, fig. 8; paralectotypes are BMNH C22683–85, all from the Upper Maastrichtian Valudavur Formation of Pondicherry, southern India.

DESCRIPTION. BMNH C93992 consists of 270° of body chamber and the nucleus of an individual with an estimated original diameter of 62 mm. Coiling is very involute, with a tiny, pitlike umbilicus, the umbilical wall subvertical and narrowly rounded. The whorl section is compressed, with whorl breadth to height ratio 0·71, the greatest breadth around mid-flank, the flanks feebly convex and subparallel, and the ventrolateral shoulders and venter evenly rounded. The surface of replaced shell and internal mould are smooth, but for a single constriction approximately 70° from the aperture. This is narrow, shallow and markedly prorsiradiate, straight on the inner flank, feebly convex on the outer flank and concave on the outermost flank. Sutures not seen.

DISCUSSION. The types of *Desmophyllites diphylloides* are all rather small (Kennedy & Henderson 1992, pl. 6, figs 1–9; pl. 16, figs 1–3, 7, 8), but Henderson and McNamara (1985: 54, pl. 4, figs 1–4) described larger specimens comparable to the present individual from the Upper Maastrichtian of Western Australia. These show constrictions that are flexuous on the flanks, as with the present material. The other Maastrichtian *Desmophyllites* is *D. larteti* (Seunes, 1892) (p. 19, pl. 12 (3), fig. 2; pl. 13 (4), figs 2, 3; see Hancock & Kennedy 1993: 154, pl. 2, figs 1–3, 10, 11, 14; pl. 3, figs 1, 4, 5), which is a larger, much more compressed species with a narrower, arched venter and much more prominent and markedly flexuous constrictions.

OCCURRENCE. The Oman specimen is from bed 21, Jebel Rawdah, section 2. Elsewhere, the species ranges from Lower Santonian to Upper Maastrichtian. There are records from southern India, Western Australia, Japan; Alaska, British Columbia, California, and Arkansas in the U.S.A.; Argentina, Angola; Pondoland and Zululand (South Africa), Tunisia, and southern France (Corbières).

Family **KOSSMATICERATIDAE** Spath, 1922
Subfamily **KOSSMATICERATINAE** Spath, 1922
Genus *BRAHMAITES* Kossmat, 1897

TYPE SPECIES. *Ammonites Brahma* Forbes, 1846: 100, pl. 8, fig. 1, by original designation.

PLATE 1

Figs 1, 2 *Desmophyllites diphylloides* (Forbes, 1846). BMNH C93992, Simsima Formation, Jebel Rawdah, section 2, bed 21.

Figs 3–7 *Pachydiscus (Pachydiscus) neubergicus neubergicus* (Hauer, 1858). **3, 4**, OUM KY 1991, from an unknown level in the Simsima Formation, southern embayment of Jebel Rawdah. **5, 6**, OUM KY 1990, from an unknown level in the Simsima Formation, southern embayment of Jebel Rawdah. **7**, OUM KY 1995, from the basal part of the Simsima Formation, Jebel Huwayyah, close to where the road cuts the north–western part of the outcrop.

All figures are × 1.

Subgenus ***ANABRAHMAITES*** Yabe & Shimizu, 1924
(= *Subbrahmaites* Yabe & Shimizu, 1924: 75).

TYPE SPECIES. *Ammonites vishnu* Forbes, 1846: 100, pl. 7, fig. 9, by original designation.

Brahmaites (Anabrahmaites) vishnu (Forbes, 1846)   Pl. 2, figs 9–14

1846   *Ammonites vishnu* Forbes: 100, pl. 7, fig. 9.
1992   *Brahmaites (Anabrahmaites) vishnu* (Forbes); Kennedy & Henderson: 418, pl. 6, figs 25, 26; pl. 9, figs 5–7, 17–20; pl. 10, fig. 5; pl. 17, figs 8, 10–11 (with full synonymy)
1993   *Brahmaites (Anabrahmaites) vishnu* (Forbes); Kennedy & Hancock: 582, pl. 1, figs 5, 6.

TYPES. Lectotype, by the subsequent designation of Kennedy & Henderson (1992: 418), is BMNH C51026, the original of Forbes 1846, pl. 7, fig. 9; BMNH C51027 is a paralectotype. Both are from the Upper Maastrichtian Valudavur Formation of Pondicherry, southern India.

DESCRIPTION. BMNH C93892 (Pl. 2, figs 11–14) consists of 200° of adult phragmocone and body chamber with a maximum preserved diameter of 83 mm, and part of the septate inner whorls, 48 mm diameter. Coiling is very evolute, the shallow umbilicus comprises 55% of diameter, with a broadly rounded umbilical wall and shoulder. The whorl section is depressed reniform, with greatest breadth just outside the umbilical shoulder, and the whorl breadth to height ratio is 1·1. The inner whorls (Pl. 2, figs 13, 14) are badly preserved, but traces of delicate crowded ribs are present on one flank. Both flanks have well-developed, prorsiradiate, deep, narrow constrictions, 2 per half whorl, flanked by a strong adapical collar-rib with feeble umbilical bulla, and a much weaker adapertural rib, the ribs extending across the venter. The outer whorl of the specimen is worn, but shows similar constrictions and collar ribs, with traces of coarse prorsiradiate flank ribs between constrictions. BMNH C93891 is a much larger body chamber fragment (Pl. 2, figs 9, 10), with maximum preserved whorl height 27·7 mm and whorl breadth to height ratio 1·0. There is a single strong constriction, flanked by a bullate adapical collar rib that persists over the venter, where it is strengthened into an incipient bulla (the specimen is worn). There is a much weaker adapertural collar-rib, and blunt non-bullate ribs, straight and prorsiradiate on the flanks, weakened and feebly convex across the venter, cover the remainder of the fragment. Sutures not seen.

DISCUSSION. These fragments are referred to *Anabrahmaites* rather than *Brahmaites sensu stricto* on the basis of the absence of bullae on intermediate ribs and the development of an incipient siphonal bulla. The inner whorls of BMNH C93892 differ in no respects from those of the paralectotype of *B. (A.) vishnu* figured by Kennedy & Henderson (1992, pl. 10, fig. 5); the outer whorls of this specimen and BMNH C93891 also find a match in the Pondicherry material (see also Stoliczka 1865, pl. 79, fig 5).

OCCURRENCE. The Oman specimens are from bed 3 or 4, Jebel Rawdah, section 1. The types are from the Upper Maastrichtian of southern India; the holotype of *Puzosia haugi* Seunes, 1892, a synonym, is from the Upper Maastrichtian *fresvillensis* Zone of southern France. The species also occurs in the Maastrichtian of northern Spain and Armenia.

Family **PACHYDISCIDAE** Spath, 1922
Genus **PACHYDISCUS** Zittel, 1884
Subgenus **PACHYDISCUS** Zittel, 1884

TYPE SPECIES. *Ammonites neubergicus* Hauer, 1858: 12, pl. 2, figs 1–3; pl. 3, figs 1, 2, by the subsequent designation of de Grossouvre 1894: 177.

Pachydiscus (Pachydiscus) dossantoi (Maury, 1930)   Pl. 3; Pl. 4, figs 1, 2

1930   *Parapachydiscus dossantoi* Maury: 136, pl. 16, fig. 1; pl. 17, figs 1, 2.
?1944   *Parapachydiscus* sp. Olsson: 107, pl. 16, fig. 1.
1985   *Pachydiscus (Pachydiscus) dossantoi* (Maury, 1930); Zaborski: 20, figs 17, 18, 20.

TYPES. Maury (1930: 136, pl. 16, fig. 1; pl. 17, figs 1, 2) based this species on a number of specimens, referring to an individual 190 mm in diameter as the type. All are from the Maastrichtian on the right bank of Rio Gramame, Fazenda do Congo, Parahyba do Norte, Brazil.

DESCRIPTION. Large, septate to whorl heights of up to 110 mm. Evolute, with 50% of previous whorl covered; umbilicus broad, shallow, with flattened, outward-inclined umbilical wall and broadly rounded umbilical shoulder. Whorl section compressed, with whorl breadth to height ratio of 0·8 in the best-preserved specimen; greatest breadth low on broadly convex flanks; outer flanks convergent; ventrolateral shoulders and venter arched. Coarse, distant ribs arise at blunt umbilical bullae, are straight and prorsiradiate across the flank, alternating regularly with shorter ribs that arise on the outer flank. Ribs sweep forwards across the ventrolateral shoulders and are weakened and broadly convex across the venter. Ornament of this type extends to the end of the phragmocone in BMNH C93895–96 and onto the body chamber in BMNH C93894. Suture poorly preserved (Pl. 3); intricately and deeply subdivided, as is typical for the genus.

DISCUSSION. Compressed whorl section plus persistence of coarse, alternately long and short ribs to a large size show these specimens to belong to *P. (P.) dossantoi*. Of other Maastrichtian species, *P. (P.) neubergicus* (Hauer, 1858) (see revision in Kennedy & Summesberger 1986), *P. (P.) gollevillensis* (d'Orbigny, 1850) (see revision in Kennedy 1986) and *P. (P.) egertoni* (Forbes, 1846) (see revision in Kennedy & Henderson 1992) are also compressed, but all are more delicately ribbed, are mature at smaller diameters, and have adult growth stages characterized by loss of outer flank and ventral ornament. *P. (P.) jacquoti* Seunes, 1890 (see revision in Kennedy 1986) has a depressed whorl section, distant ribs and effacement of outer flank and ventral ornament on the phragmocone.

OCCURRENCE. Most of the Oman specimens come from the lower *Loftusia*-rich beds at Jebel Huwayyah. BMNH C93894 comes from bed 10 or 11, section 1, Jebel Huwayyah, while C93895 comes from bed 10. OUM K1998 (= Skelton 84/32·2) is also from Jebel Huwayyah, section 1, from an unspecified level. One specimen, BMNH C93896, comes from a loose block derived from the basal bed of the Simsima Formation at Jebel Buhays, section 1. The type occurrence is of Maastrich-

tian age, but is difficult to place more precisely within the stage. Kennedy (1986: 44) regarded *Pachydiscus sumneri* Maury, 1930 (p. 155, pl. 13, figs 1, 2), *Parapachydiscus poseidon* Maury, 1930 (p. 155, pl. 15) and *Canadoceras riogramense* Maury, 1930 (p. 169, pl. 21, fig. 2), which are said to occur in the same unit as *P. (P.) dossantoi*, as possible synonyms of the Upper Maastrichtian *Anapachydiscus fresvillensis* (Seunes, 1890). The original figures are so poor, however, and the relative position of species within Maury's 'grey limestone' is unknown, so that only the *possibility* of an Upper Maastrichtian date can be considered. *P. (P.) dossantoi* from Nigeria (Zaborski 1983, 1985) comes from the Nkoporo Shale, and was regarded as 'probably Lower Maastrichtian' (no definition of the Lower/Upper Maastrichtian boundary was given). It co-occurs with *Gaudryceras beantalyense* Collignon, 1956, *Baculites* sp. and *Sphenodiscus lobatus costatus* Zaborski, 1982. On this evidence it can be dated no more precisely than Maastrichtian.

Pachydiscus (Pachydiscus) neubergicus neubergicus
(Hauer, 1858)   Plate 1, figs 3–7

1858   *Ammonites neubergicus* Hauer: 12 (*pars*), pl. 2, figs 1–3 (*non* pl. 3, figs 1, 2).
1993   *Pachydiscus (Pachydiscus) neubergicus neubergicus* (Hauer, 1858); Hancock & Kennedy: 158, pl. 3, figs 6, 7; pl. 9, figs 5–8; pl. 12, figs 7–9; pl. 13, figs 5–7 (with synonymy).

TYPES. Lectotype, by the subsequent designation of de Grossouvre 1894: 209, is no 1858.01.6 in the collections of the Geologisches Bundesanstalt, Vienna; three paralectotypes bear the same number, and all are from the Lower Maastrichtian of Neuberg, Steiermark, Austria.

DESCRIPTION. The best-preserved specimen is OUM KY 1990 (Pl. 1, figs 5, 6), an internal mould of a phragmocone 93 mm in diameter. Coiling is fairly involute, the umbilicus small, with a flattened, subvertical low wall and narrowly rounded umbilical shoulder. The whorl section is compressed, with a whorl breadth to height ratio of 0·74, the greatest breadth below mid-flank, inner flanks feebly convex, outer flanks flattened and convergent, ventrolateral shoulders broadly rounded, and the venter only feebly convex. There are an estimated 14 umbilical bullae per whorl. These give rise to single ribs, sometimes feebly concave on the innermost flank. They are prorsiradiate and weak across the flanks, where long and short intercalated ribs are inserted, so that there are many more coarse concave ribs at the ventrolateral shoulder, although the number per whorl cannot be determined. OUM KY1994 is a worn but conspecific fragment of phragmocone with a maximum preserved whorl

height of 36 mm and whorl breadth to height ratio of approximately 0·89.

OUM K1991–93 are fragments of body chamber (Pl. 1, figs 3, 4), with a maximum preserved whorl height of 51·5 mm and whorl breadth to height ratio of 0·75. At the adapical end of the fragment strong bullate primary ribs at the umbilical shoulder correspond to 3–4 times as many ribs at the ventrolateral shoulder. On the adapical part of the fragment the secondary ribs are lost, and the ornament is of distant primaries that efface across the flanks. OUM K1995 (Pl. 1, fig. 7) is a very worn individual 150 mm in diameter, probably adult, with a phragmocone diameter of 110 mm and whorl breadth to height ratio of 0·78. There appear to be 14–16 primary ribs per whorl, and more numerous primary plus secondary ribs at the ventrolateral shoulder. Sutures not seen.

DISCUSSION. Coiling, whorl proportions and ribbing show these specimens to belong to the *Pachydiscus (P.) neubergicus neubergicus* (Hauer, 1858) – *P. (P.) gollevillensis* (d'Orbigny, 1850) group. Topotypes of the former generally have 14–17 umbilical bullae and 58–60 ventral ribs per whorl (Kennedy & Summesberger 1986), the latter 9–11 umbilical bullae and approximately 80 ventral ribs (Kennedy, 1986), suggesting the present material belongs to the former. Nuclei of *P. (P.) neubergicus neubergicus* and *P. (P.) neubergicus dissitus* Henderson & McNamara, 1985, are identical, but the latter has a mature ornament with many ventral ribs (Henderson & McNamara 1985, pl. 7, fig. 7), not seen in the present material (Pl. 1, figs 3, 4), which are thus referred to the nominate subspecies.

OCCURRENCE. OUM KY1990, 1991–93 (1 specimen) and KY 1994 were collected in the southern embayment of Jebel Rawdah. Their position in the succession is unknown. KY1995 comes from the lower part of the Simsima formation in the north-western part of Jebel Huwayyah, close to where the road cuts the outcrop. Elsewhere the species first appears low in the Lower Maastrichtian, and is best known from the Lower Maastrichtian of Austria, Poland, Ukraine, Armenia, Russia, SW France, northern Spain, Nigeria, Brazil and Zululand (South Africa). It occurs in the lower Upper Maastrichtian of Denmark, and the Upper Maastrichtian of southern India.

Indeterminate pachydiscid

DISCUSSION. BMNH C93987 is a fragmentary pachydiscid, still septate at a whorl height of 150 mm. It bears distant primary ribs, but is indeterminate even as to genus.

OCCURRENCE. The specimen comes from the gritty calcareous bed (bed 9), of the Qahlah Formation, immediately

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PLATE 2

Figs 1–3, 15, 16   *Lewyites ambindense* (Collignon, 1971). **13**, BMNH C93890; from the *Loftusia*-rich beds, Qahlah Formation, Jebel Huwayyah, section 1, bed 10 or 11. **15, 16**, OUM KY1996; from the basal part of the Simsima Formation, north-western Jebel Huwayyah, close to where the road cuts the outcrop.

Figs 4–8   *Nostoceras (Nostoceras) major* Kennedy and Cobban, 1993. **4–6**, BMNH C93994, from beds 10 or 11, Qahlah Formation, Jebel Huwayyah, section 1; **7, 8**, BMNH C93993, Basal Simsima Formation, bed 9, Jebel Bu Milh, section 2.

Figs 9–14   *Brahmaites (Anabrahmaites) vishnu* (Forbes, 1846). **9, 10**, BMNH C93891; **11–14,** BMNH C93892. Both from the Simsima Formation, bed 3 or 4, Jebel Rawdah, section 1.

Figs 17–19   *Libycoceras*? sp., BMNH C93887, from the conglomeratic basal bed of the Simsima Formation, Jebel Buhays, section 2.

Fig 20   *Nostoceras (Nostoceras)* sp., BMNH C93888, from bed 6, Jebel Huwayyah, section 2.

All figures are × 1
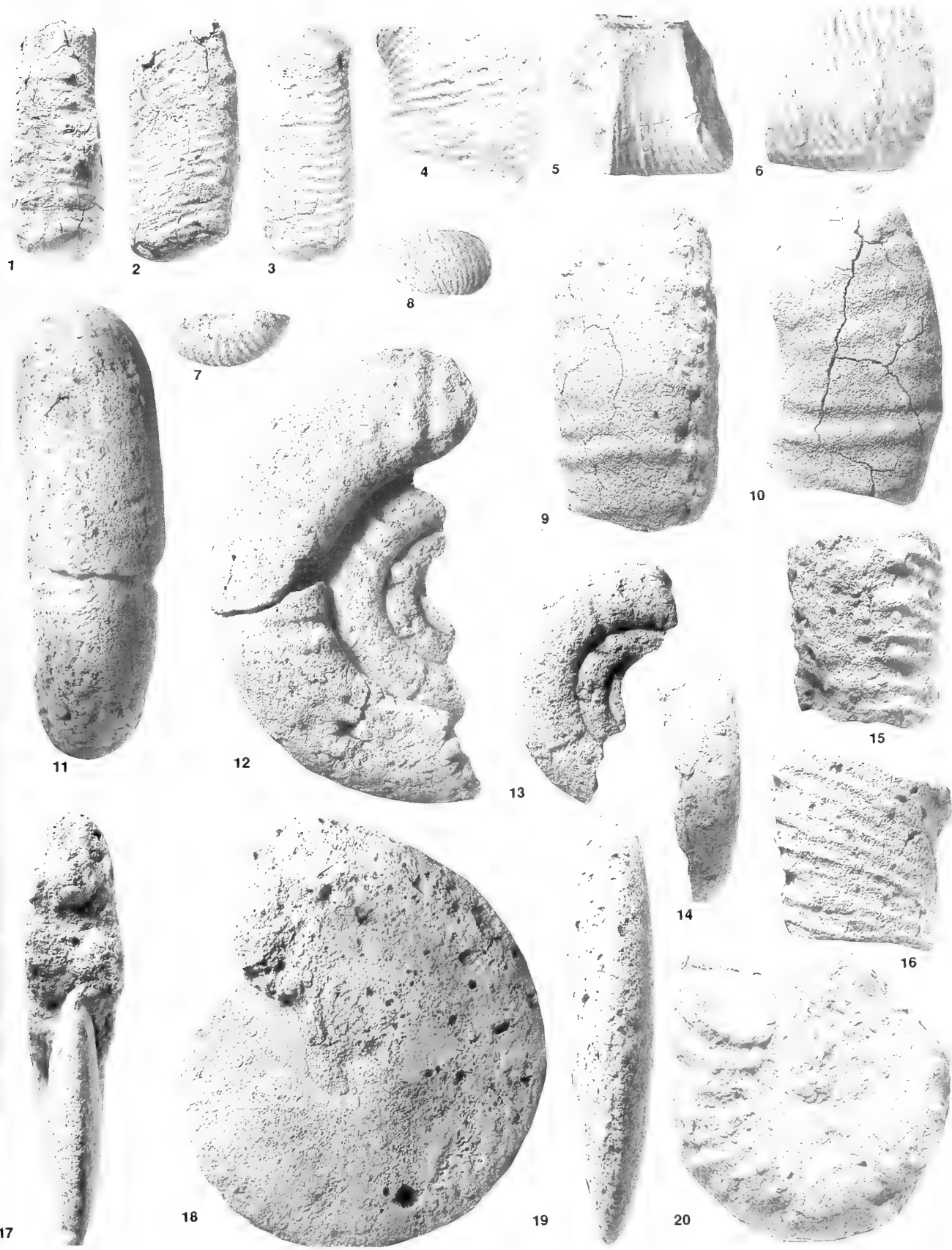
PLATE 3
Pachydiscus (Pachydiscus) dossantoi (Maury, 1930). BMNH C93896, from the basal bed of the Simsima Formation, Jebel Buhays, section 1;
  slightly reduced.

below the *Loftusia*-rich beds at Jebel Huwayyah, section 1.

Superfamily **ACANTHOCERATACEAE** de Grossouvre,
1894
Family **SPHENODISCIDAE** Hyatt, 1900
(= Libycoceratidae Zaborski, 1982: 306)
Genus *LIBYCOCERAS* Hyatt, 1900

TYPE SPECIES. *Sphenodiscus ismaelis* Zittel, 1895, p. 451,
text-fig. 631, by original designation.

Libycoceras ? sp.   Plate 2, figs 17–19

DESCRIPTION. BMNH C93887 is a very corroded internal
mould of a small adult with 240° of body chamber preserved
and a maximum diameter of 80 mm. The phragmocone is
oxycone, with a whorl breadth to height ratio of 0·4. The
body chamber develops subparallel flanks, and the venter
rounds progressively; the whorl breadth to height ratio is 0·39
at the aperture. No ornament is preserved on the heavily
corroded surface, other than a faint trace of low ribs on the
outer flank. The suture (Text-fig. 1) shows a well-developed
adventitious lobe in the first lateral saddle, the ventral
saddles are feebly indented, and the umbilical saddle is
entire.

DISCUSSION. This poorly preserved specimen is referred to
Libycoceras? rather than *Sphenodiscus* on the basis of its
sutural characteristics; it is specifically indeterminate.

OCCURRENCE. BMNH C93887 is from the basal conglomer-
atic bed of the Simsima Formation at Jebel Buhays, section 2.
Species of *Libycoceras* first occur in the Upper Campanian
and may range into the Lower Maastrichtian (Zaborski
1982).

Suborder **ANCYLOCERATINA** Wiedmann, 1966
Superfamily **TURRILITACEAE** Gill, 1871
Family **DIPLOMOCERATIDAE** Spath, 1926
(= Neocrioceratinae Spath, 1953)
Subfamily **DIPLOMOCERATINAE** Spath, 1926
(= Scalaritinae Ward, 1976: 455)
Genus *GLYPTOXOCERAS* Spath, 1925
(= *Neohamites* Brunnschweiler, 1966)

TYPE SPECIES. *Hamites rugatus* Forbes, 1846: 116, pl. 11, fig.
6, by original designation (Spath 1925: 30, as *Hamites (Aniso-
ceras) rugatus* (Forbes) Kossmat).
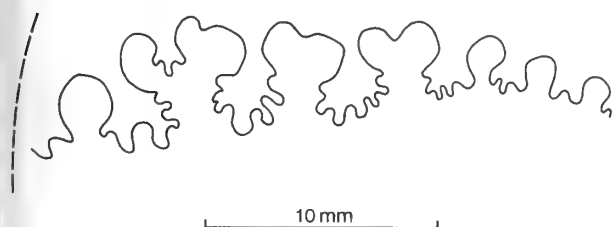
Fig. 1 Idealised suture of *Libycoceras*? sp., based on BMNH
C93887, a badly corroded specimen.

Glyptoxoceras sp.

DESCRIPTION AND DISCUSSION. BMNH C93889 is a straight
fragment with a whorl height of 6·5 mm, the whorl section is
compressed oval, with strong even prorsiradiate flank ribs,
transverse on the venter and weakened on the dorsum. It is
specifically indeterminate, but ribbing and coiling suggest
that it is a *Glyptoxoceras*, a genus recorded from Lower
Santonian to Upper Maastrichtian.

OCCURRENCE. BMNH C93889 is from the basal 60 cm shell
bed immediately overlying unweathered ophiolite (bed 1) at
Jebel Aqabah.

Genus *LEWYITES* Matsumoto & Miyauchi, 1984

TYPE SPECIES. *Idiohamites* (?) *oronensis* Lewy, 1969: 127, pl.
3, figs 10, 11, by original designation.

Lewyites ambindense (Collignon, 1971) Plate 2, figs 13,
15, 16

1971   *Neancyloceras ambindense* Collignon: 11, pl. 644, fig.
2380.

TYPE. Holotype, by monotypy, is the original of Collignon
1971, pl. 644, fig. 2380, from the Maastrichtian of locality 504
of Collignon, Mont Ambinda-Mikoboko (Manera), Mada-
gascar.

DESCRIPTION. BMNH C93890 is a 45 mm long fragment of a
straight shaft showing slight curvature at the adapical end.
The fragment is wholly septate, with traces of recrystallized
shell. The whorl section is compressed oval, with a whorl
breadth to height ratio of 0·9 and maximum preserved whorl
height of 20 mm. There are 11 ribs in a distance equal to the
whorl height. They are narrower than the interspaces, sharp,
transverse to feebly convex on the dorsum, sweeping for-
wards and feebly convex on the dorsolateral margin, mark-
edly prorsiradiate and strengthening across the flank, and
transverse on venter. Alternate ribs bear small ventral clavi;
occasionaly a second rib is feebly linked to a clavus. Much
larger is OUM KY1996, a body chamber fragment with a
maximum preserved whorl height of 29 mm. Ornament is as
in the smaller specimen, but for the marked effacement of
ribs on the dorsum of the internal mould. Sutures not seen.

DISCUSSION. I was unable to trace the holotype of *Neancylo-
ceras ambindense* during a recent examination of the Colli-
gnon Collection, housed in the Université de Bourgogne,
Dijon. The ribs of the Oman material are more markedly
prorsiradiate than in the holotype, with fewer non-
tuberculate ribs, but they are otherwise similar. Reference to
Lewyites is based on a comparison with topotypes of the
type species in the Oxford University Museum (OUM
KY2021–25), and large fragments from New Jersey figured
by Cobban (1974, pl. 10, figs 22–35) and Kennedy & Cobban
(1993b, figs 5.1–5.18, 5.22–5.26; 7.19, 7.20; 9.4, 9.7).

OCCURRENCE. BMNH C93890 is from bed 10, Jebel
Huwayyah, section 1. OUM K1996 (Skelton 84/16·2) comes
from the basal part of the Simsima Formation of the north-
western part of Jebel Huwayyah, close to where the section is
cut by the road. The holotype is from the so-called Lower
Maastrichtian Zone à *Pachydiscus gollevillensis* et *P. neuber-
gicus* of Collignon, but associated ammonites from the type
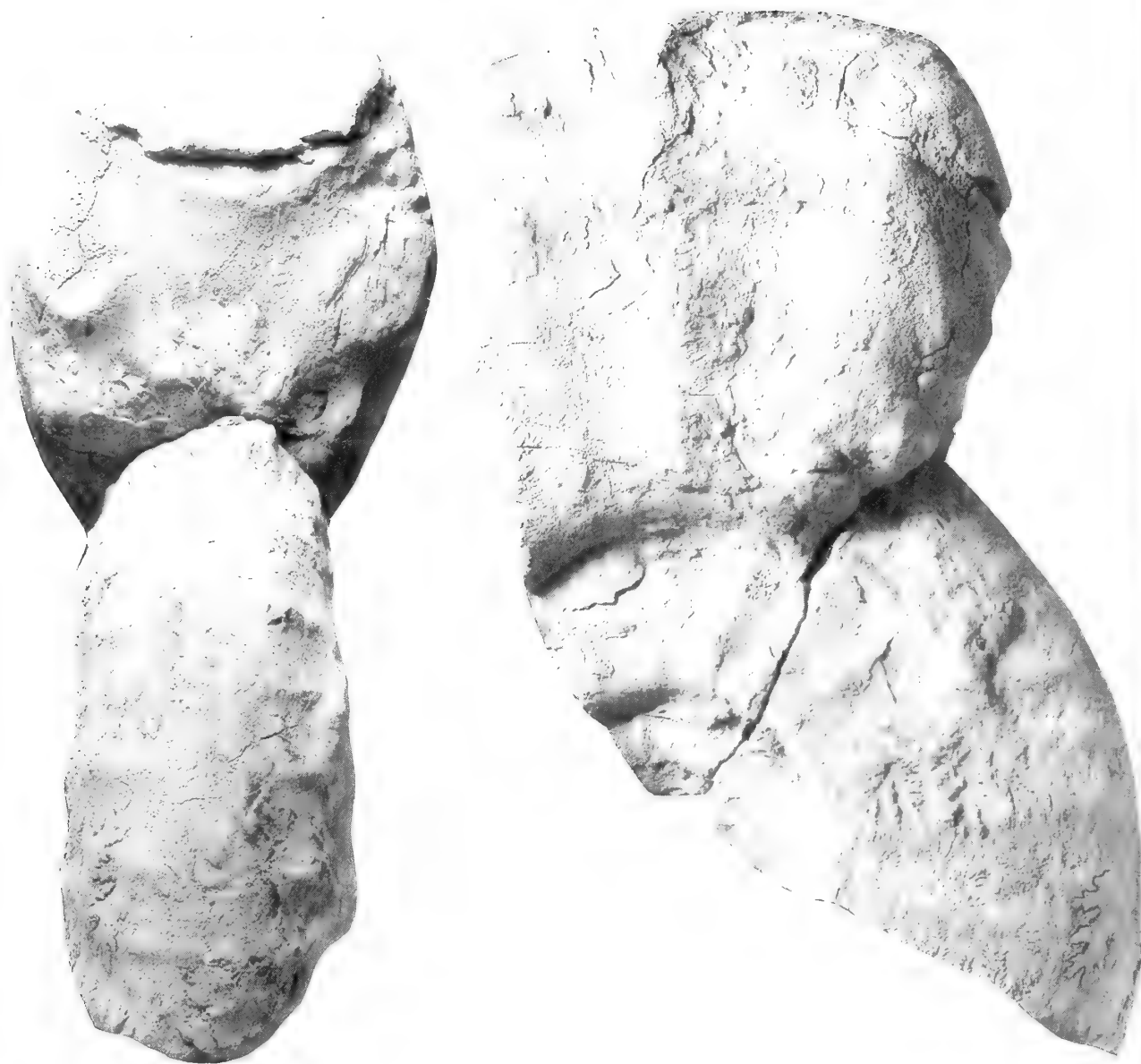
locality in the Collignon Collection indicate Upper Maastrich-
tian only.

Family **NOSTOCERATIDAE** Hyatt, 1894
(= Jouaniceratidae Wright, 1952: 218; Bostrychoceratinae
Spath, 1953: 16;
Emperoceratinae Spath, 1953: 17; Hyphantoceratinae Spath,
1953: 16)
Genus *NOSTOCERAS* Hyatt, 1894
Subgenus *NOSTOCERAS* Hyatt, 1894

TYPE SPECIES. *Nostoceras stantoni* Hyatt, 1894: 569 (=
Ammonites approximans Conrad, 1855: 266), by original
designation.

Nostoceras (Nostoceras) major Kennedy & Cobban,
1993   Plate 2, figs 4–8

1993c   *Nostoceras (Nostoceras) major* Kennedy & Cobban:
6·1, fig. 4.

TYPE. Holotype in Texas Memorial Museum Collections no
77981, from the Upper Maastrichtian Corsicana Formation
1·2 km (0·75 miles) SE of New Sweden, Travis County,
Texas.

DESCRIPTION. There are 2 fragments, BMNH C93993, with a
whorl height of 13 mm, and BMNH C93994, with a whorl
height of 39·5 mm. Both are derived from helices with the
whorls in tight contact, there being a shallow concave

impressed zone on the upper whorl face; the outer and lower whorl faces are broadly convex, the inner whorl face is flattened. Ornament is effaced on the impressed zone of the upper whorl face, but wiry narrow ribs strengthen, sweep back and are concave across the juncture of upper and outer whorl faces and are markedly prorsiradiate and narrower than the interspaces on the outer whorl face, sweeping backwards and feebly concave across the juncture of outer and lower whorl faces, straight and prorsiradiate on the lower whorl face and convex and effaced on the inner. All ribs are single on the larger fragment, but occasionally join in pairs at the juncture of outer and lower whorl faces in the smaller fragment. Sutures not seen.

DISCUSSION. The simple coiling and ornament of these fragments occurs in nostoceratids from the Turonian onwards. Given the Maastrichtian age of the specimens, reference to *Nostoceras (Nostoceras)* is indicated. The fragments differ in no significant respect from the holotype of *N. (N.) major*, other than their coiling direction, absence of flared ribs and constrictions, possibly reflecting no more than the short lengths preserved, there being only 2–3 constrictions and associated flared ribs per whorl in the type.

OCCURRENCE. BMNH C93993 comes from bed 9, Jebel Bu Milh, section 2: C93994 comes from bed 10 or 11, Jebel Huwayyah, section 1. The holotype is from the Upper Maastrichtian of Texas.

Nostoceras (Nostoceras) sp.   Plate 2, fig. 20

DESCRIPTION AND DISCUSSION. BMNH C93888 is an poorly preserved U-shaped body chamber with a maximum preserved whorl height of 21 mm. Ornament is of coarse single ribs with traces of ventral tubercles on at least some ribs. The specimen is specifically indeterminate, but recalls the *Nostoceras (N.) hyatti* group, of the uppermost Campanian Lower Maastrichtian (Kennedy & Cobban 1993b).

OCCURRENCE. The specimen comes from bed 6, Jebel Huwayyah, section 2.

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Maastrichtian nautiloids from the United Arab Emirates-Oman border region

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SYNOPSIS. The two nautiloids *Deltoidonautilus salisfilius* sp. nov. and *Cimomia* aff. *sowerbyana* (d'Orbigny) are described from the Maastrichtian Simsima Formation of the United Arab Emirates and Oman.

INTRODUCTION

Cephalopods form only a tiny percentage of the macrofossils collected from the late Cretaceous of the Emirates-Oman border area. They consist only of ammonites and nautiloids and, in spite of the small numbers, it is apparent that the distribution of the two groups is rather different and may reflect their partial ecological separation.

Two distinct species of nautiloids were collected from a number of the Maastrichtian localities on the Emirates-Oman borders. The possibility that they might have been sexual dimorphs is discounted because there are no features in common between the two. For instance, the change in shape on the final whorl of the smaller species does not occur on the larger species.

The nautiloids contrast with those described by Noetling from the Late Cretaceous of the Mari Hills (Pakistan), where species of *Cimomia* and *Deltoidonautilus* do not seem to occur (Noetling 1897).

There seems to be little change in the relatively low nautiloid diversity after the end of the Cretaceous. The apparent loss of *Cymatoceras* is matched by the increase in the Hercoglossidae, mostly in the form of the new suture-line pattern of *Hercoglossa*. This change in shell architecture could represent a wider range of depth tolerance within the superfamily.

SYSTEMATIC DESCRIPTIONS

Superfamily *NAUTILOIDEA* de Blainville, 1824
[Name elevated from family rank, Shimanskiy, 1957]
Family **HERCOGLOSSIDAE** Spath, 1927

The distinction between some of the genera in this family is rather dubious: *Cimomia* and *Deltoidonautilus* in particular seem to overlap. Kummel (1964, K456) suggests that *Cimomia* is 'a morphologically transitional form between *Eutrephoceras* and *Hercoglossa*'. Both *Cimomia* and *Deltoidonautilus*, if indeed they are distinct, seem to foreshadow *Nautilus* itself in their shell morphology.

Genus *DELTOIDONAUTILUS* Spath, 1927

TYPE SPECIES. *Nautilus sowerbyi* J. de C. Sowerby, 1843 (see footnote by Kummel, 1964: K456–57), from the Lower Eocene, London Clay.

SYNONYMY. *Deltoidonautilus* may yet prove to be a junior synonym of *Angulithes* de Montfort, 1808, because of the various intrepretations of the type species of *Angulithes*, *Nautilus triangularis* de Montfort, 1802. Kummel accepted the name in 1956 but rejected it as a *nomen dubium* in the *Treatise* (1964). It is not clear in de Montfort's (1808: 8) description, whether the type specimen came from the Lower Kimmeridgian or from the Cenomanian. It is beyond the scope of the present work to establish the type material of this taxon, with the result that Kummel's (1964: K456) later opinion that *Angulithes* should be treated as a *nomen dubium* is followed here.

DESCRIPTION. Characteristically smooth, involute and often compressed with a sub-carinate venter in early to middle growth stages. Suture sinuous and projected forwards on the venter. Distinguished from *Cimomia* by the carinate venter.

RANGE. Upper Cretaceous (Cenomanian) to Oligocene; cosmopolitan.

Deltoidonautilus salisfilius sp. nov.   Plate 1, figs 1–3

?1861   *Nautilus rota* Blandford: pl. 25, fig. 2 only.
 1928   *Nautilus jordani* Zittel; Lees: 663, pl. 44, fig. 6.

HOLOTYPE. BM C.59590, from the 'Main Gastropod Bed', bed 6, at Jebel Bu Milh (JBM 2), NNW of Al Ain; base of Simsima Formation, Maastrichtian, probably Lower Maastrichtian.

OTHER MATERIAL. Thirteen paratypes from the same locality and horizon, BM C.59591–603, Morris and Smith Collection. Three additional paratypes apparently from the same locality and horizon, G.M.Lees collection (mentioned Lees, 1928), BM C.31034–36. Two specimens from the basal 2 meters of the Simsima Formation at Jebel Faiyah (JF2), U.A.E., BM C.59607–08. ?Lower Maastrichtian, Morris and Smith Collection. One specimen from Jebel Faiyah (JF1b), loose, but probably from the basal Simsima Formation, ?Lower Maastrichtian, Gale, Morris and Smith collection, BM C.59609. One specimen from Jebel Buhays (JB1b) also loose but ?basal Simsima Formation, Gale, Morris and Smith collection, BM C.59610. All the specimens found apparently occur

just above the flooding surface at the base of the Simsima Formation, probably at a similar horizon to *Libycoceras* sp. and *Nostoceras* spp.

DESCRIPTION. Shell rather small, the two near complete specimens from Jebel bu Milh are both approximately 102 mm in diameter. Shell planospiral, smooth, involute, non-umbilicate on outer shell surface; internal mould with a narrow, shallow umbilicus. Compressed, discoidal, sub-oxycone with rounded to subcarinate venter on inner and middle whorls; outer whorl, ie. body-chamber, rounded and much less compressed, occupying approximately one third of the last whorl. Siphuncle well dorsal of centre. Suture with well-rounded but relatively narrow ventral saddle that bends forward towards the aperture in a way that is more prominent in the sub-oxycone stages than in the more rounded whorls where the few final sutures occur; broad, shallow, sub-symmetrical lateral lobe; relatively low, smallish lateral saddle close to the umbilical margin. Sutures show consider-able crowding towards the body-chamber in what seems to be a fully grown individual. Siphonal sinus moderate on the penultimate whorl, observed only on specimen BM C.31034.

COMPARISON WITH OTHER SPECIES. *Nautilus fleuriausianus* d'Orbigny (1840: 82, pl. 15) has a rounded venter similar to the body-chamber of the present species, but does not have the earlier, more oxycone stage. It is apparently of Upper Cenomanian age from the 'craie à Caprines' at Ile Madame, Charente, France. It may prove to be a more rounded specimen of the widespread species named *Nautilus triangu-laris* (de Montfort; d'Orbigny, 1840: pl. 12; ? = *Angulithes triangularis* de Montfort 1808). Two nearly complete speci-mens from the Cenomanian of Sidmouth (BM C.931), and from the Upper Grey Chalk near Folkestone (BM C.8320), are both carinate and show no sign of change to a round ventered body-chamber at approximately 160 mm and 180 mm diameter respectively. *Nautilus mermeti* Coquand, 1862, from Algeria, may also prove to be a synonym of this Cenomanian species.

Nautilus westphalicus Schlüter, 1876 from the Late Santo-nian or Lower Campanian Quadraten Kreide from Dulmen in Germany also has a carinate body-chamber. *Nautilus galea* Fritsch, 1872, from the Iserschichten in Bohemia, has a carinate venter on the body chamber, has much broader whorls and apparently has less sinuous sutures.

There may be three separate taxa amongst Blanford's (1861) illustrations of his species *Nautilus rota*: his pl. 24 fig. 3 and pl. 25, fig. 1 clearly belong to *Cymatoceras*, while the smooth internal mould of his pl. 25, fig.2 has the flexed suture typical of *Deltoidonautilus* and could well belong in the present species.

Genus *CIMOMIA* Conrad, 1866

TYPE SPECIES. *Nautilus burtini* Galeotti, 1837, from the Eocene of Belgium (a very similar species to *C. imperialis* (J. Sowerby, 1812)).

Cimomia aff. *sowerbyana* (d'Orbigny, 1840)   Plate 1, fig. 4; Plate 2

aff. 1840   *Nautilus sowerbyanus* d'Orbigny: 83, pl. 16.
aff. 1850   *Nautilus sowerbyanus* d'Orbigny; d'Orbigny: 189.
1902   *Nautilus jordani* Wanner: 143, pl. 19, fig. 21.
1956   *Cimomia jordani* (Wanner); Kummel: 451.

MATERIAL. A single fairly well-preserved specimen, BM C.59611, from the base of the Simsima Formation at Jebel Fayah (JF 2), associated with *Deltoidonautilus salisfilius* sp. nov.; the body chamber is missing. A single poorly preserved but virtually complete specimen from Jebel Buhays (JB 1b), also apparently from the base of the Simsima Formation, BM C.59612. Three doubtful specimens from Jebel Rawdah (JH 1), one of them *in situ* in the base of bed 5, BM C.59613, and the other two loose on the scree below but apparently from the same horizon, BM C.59614–15.

In his original description, d'Orbigny stated that the local-ity of the type specimen of *Nautilus sowerbyanus* was unknown, but later, in the *Prodrome* (d'Orbigny, 1850: 189), he gave the locality as Montrichard, France. The specimen was in the Musée d'Histoire Naturelle, Paris, the locality details having been sent by M. Cordier, and it seems quite likely that Fischer, who organised d'Orbigny's collection, must have sorted out the locality before publication of the *Prodrome*.

Wanner's holotype of *Nautilus jordani* came from the uppermost white chalk near Bab-el-Jasmund to the north of Dachel, western Egypt.

DESCRIPTION. Shell medium-sized, planospiral, smooth, involute. External shell non-umbilicate, with the umbilicus of the internal mould plugged by a slight recurved extension of the lateral saddle, almost in the form of a small very shallow lobe. Shell inflated to spheroidal with flanks converging to the rounded but slightly flattened venter. Suture with a very low, gently rounded ventral saddle, a symmetrical, relatively shallow lateral lobe and a relatively prominent well-rounded lateral saddle.

COMPARISON WITH OTHER SPECIES. ?*Cimomia applanatus* (Wanner, 1902: 143), another species named from western Egypt, could be another variant of this species but is consid-erably more evolute than any of the specimens considered here from the same area. The identification of *Nautilus desertorum* Quaas (1902: 299) is also uncertain, because it is not possible to judge from the original illustration whether the suture-line is sinuous like that of *Cimomia* or straighter like that of *Eutrephoceras*.

Cimomia aff. *sowerbyana* is similar in general shape to *Nautilus sublaevigatus* d'Orbigny (1850: 189; *nom. nov.* for *N. laevigatus* d'Orbigny, 1840: pl. 17, *non* Reinecke, 1818). The first locality listed where d'Orbigny collected this species is Martrou near Rochefort. He also listed a number of other localities including Montrichard, Uchaux and several from Cotentin; these span a range from Turonian to Maastrichtian. The sutures of *N. sublaevigatus* seem much less sinuous than those of *Cimomia sowerbyana* and suggest that this species

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PLATE 1
Figs 1–3   *Deltoidonautilus salisfilius* sp. nov. Base of Simsima Formation Maastrichtian, ? Lower Maastrichtian, Jebel Bu Mil;ch, NNW of Al Ain. **1**, holotype, BM C.59590; **2**, paratype, BM C.59591; **3**, paratype, BM C.59592, arrow shows poistion of the siphuncle; all × 1.
Fig. 4   *Cimomia* aff. *sowerbyana* (d'Orbigny, 1840). Base of Simsima Formation, ?Lower Maastrichtian, Jebel Fayah, south of Dayid, ventral view; BM C.59611; × 1.
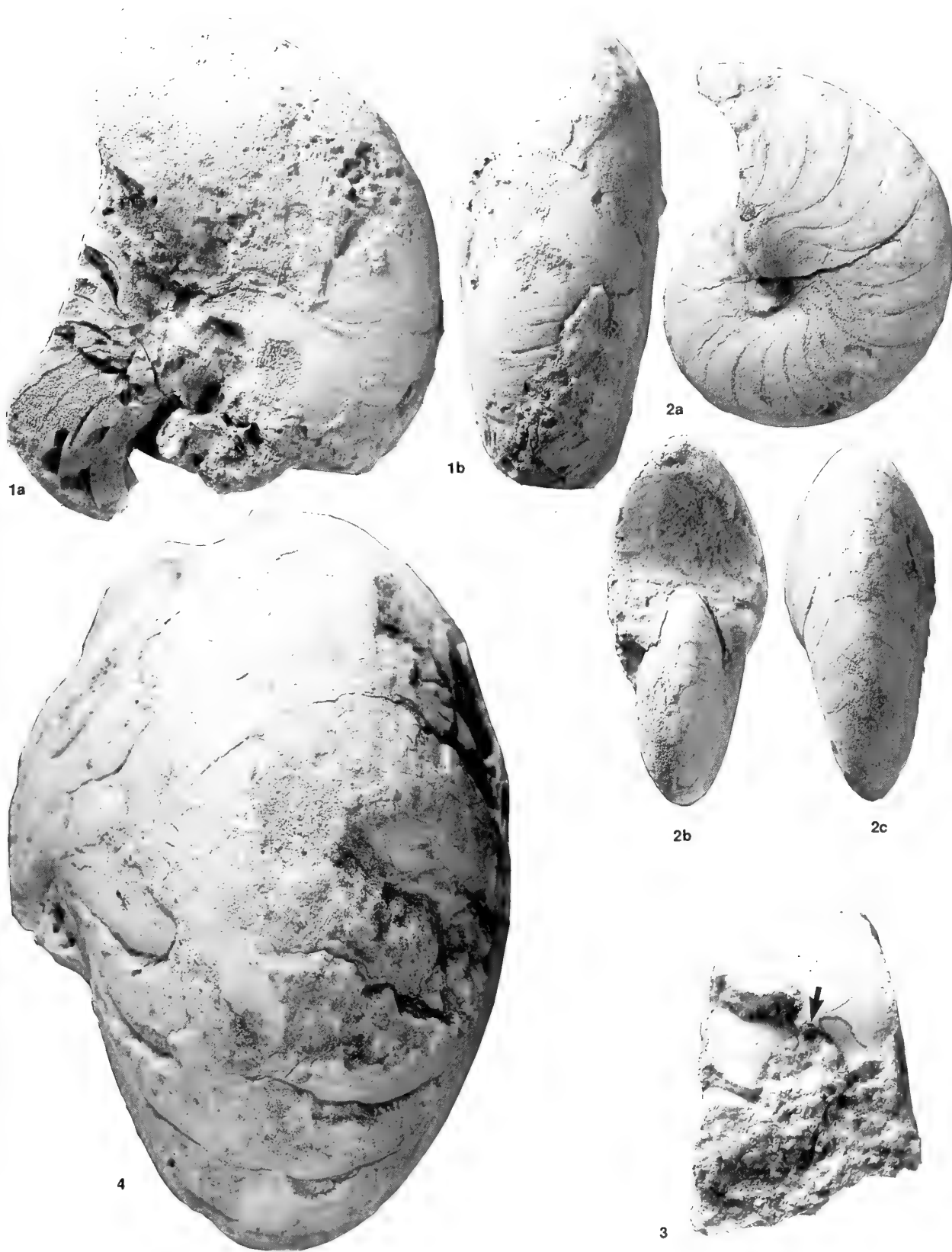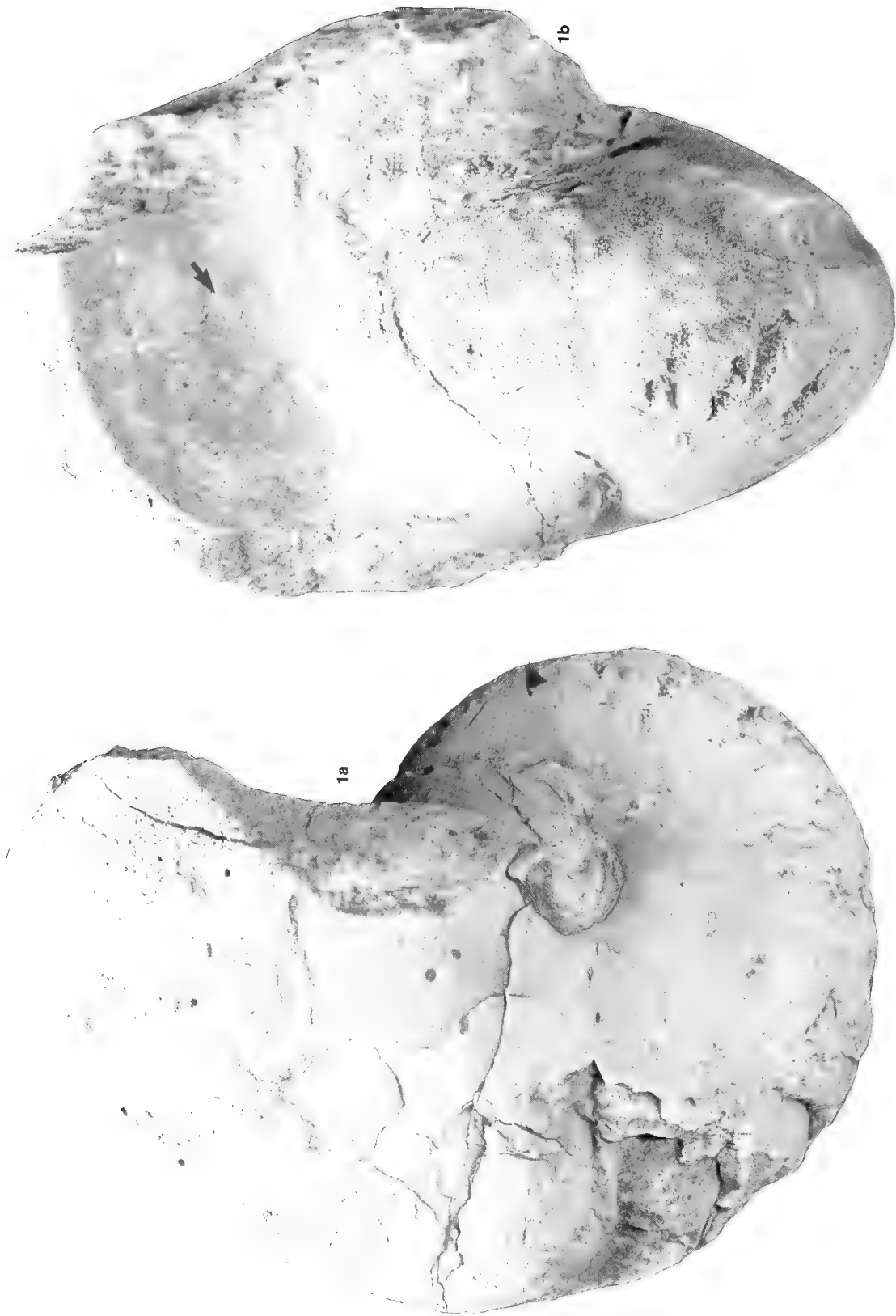
PLATE 2

Cimomia aff. sowerbyana (d'Orbigny, 1840). Base of Simsima Formation, (?Lower) Maastrichtian, Jebel Fayah, south of Dayid; BM C.59611: **1a**, side view; **1b**, apertural view; arrow shows the position of the siphuncle; × 0·75.

belongs to *Eutrephoceras*. Similarly *N. vastus* Kner, 1850, *Cimomia* cf. *forbesi* d'Archiac & Haime, 1854 (a Danian species), and *Eutrephoceras sphaericus* (Forbes, 1846) (holotype from Pondicherry, India, BM C.73524; not pre-occupied by *Nautilites sphaericus* Martin, 1809), may belong to *Eutrephoceras*.

A number of Late Cretaceous specimens in the BM(NH) collection from the United States also indicate that *Nautilus dekayi* Morton, 1833, does not have the sinuous suture-line of *Cimomia* and properly belongs in *Eutrephoceras*.

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Maastrichtian Inoceramidae from the United Arab Emirates-Oman border region

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SYNOPSIS. Descriptions of Inoceramids from Upper Cretaceous post-Semail Nappe emplacement deposits include *Endocostea (Selenoceramus) semaili* sp. nov. Most specimens are from the Simsima Formation in Jebel Rawdah, immediately below the massive limestone facies, and they indicate a mid-Maastrichtian age.

INTRODUCTION

Small collections of Inoceramidae from two localities on the western edge of the Omani Mountains, close to the border between the United Arab Emirates and Oman, are preserved largely as uncrushed internal moulds. The first is from the Simsima Formation in Jebel Rawdah just north of the Al Ain to Hatta Road, about 10 Km east of the Madam Roundabout, just east of the Omani Border Post, and is of mid-Maastrichtian age. The second is from the *Loftusia*-rich marls below the Simsima Formation in Jebel HuwaYyah (known as Fossil Valley), to the east and north-east of Al Ain, and is apparently of Lower Maastrichtian age. It is quite clear that the specimens from the higher horizon, i.e. in Jebel Rawdah, assist with the age determination of the strata, and they may have potential for international correlation.

The Inoceramidae show that at least three distinct lineages existed in the eastern Arabian area in mid-Maastrichtian times. Each lineage seems to fall in some part of Whitfield's (1877) genus, *Endocostea*, which is in much need of revision. Any serious revision is, however, beyond the scope of this paper. Subgeneric names are used tentatively until we have a better understanding of the phylogeny of the group. The apparent lack of specimens of *Trochoceramus*, which is widespread across Africa in late Campanian and Maastrichtian times, may reflect the palaeoecology. The water may have been either too shallow or too warm, or the sediment too coarse.

The specimens described here were collected by Drs Gale, Morris and Smith in January 1992, by Drs Nolan and Skelton during an earlier visit (Nolan *et al.* 1990), and by members of the Emirates Natural History Group.

Class **BIVALVIA** Linnaeus 1758
Subclass **PTERIOMORPHIA** Beurlen, 1944
[*nom. trans.* Newell, 1965]
Superfamily **INOCERAMOIDEA** Giebel, 1852
[?=Ambonychioidea Miller, 1877]

The Inoceramidae share with *Ambonychia* the thick calcitic inter-umbonal ligament area not present in adult Pterioidea.

Family **INOCERAMIDAE** Giebel, 1852

DESCRIPTION. Variously shaped, concentrically lamellose or plicated or radially plicated *Pteria*-like bivalves which sometimes grew to a large size. The outer calcareous shell layer consists of vertical calcite prisms which are modified to pyriform laths on the ligament area. The ligament, usually multivincular, is attached largely to this external layer; inner shell layer nacreous; usually lacking hinge teeth; usually equivalve or subequivalve, some species inaequivalved. A complex of muscle scars close to the umbones is consistant with byssal fixation. Apparently monomyarian with the posterior adductor often close to the posterior ventral margins but often obscure. It is very difficult to be certain whether an isolated muscle scar situated about halfway below the umbones and towards the anterior margin is a large pedal muscle scar or a small anterior adductor. The Inoceramidae became extinct by the beginning of the Tertiary.

COMMENTS. The ligament area of these later Cretaceous species is seldom well-exposed and the pits characteristic of earlier species have only been observed on one of the species. It remains possible that lineages other than *Tenuipteria* (Dhondt, 1983b) have no pits for the differing ligament types.

THE INTERNAL SHELL RIB. Many post-Coniacian Inoceramidae have an internal shell rib, sillon or Hohlkehle. The nature of this internal rib has been discussed on a number of occasions (especially Seitz, 1967: 14–41). It occurs commonly in a number of Inoceramidae from at least as early as the Santonian. It is here considered to be an architectural character of the shell, and it is clearly variable in some of the taxa that have it. Two specimens of *Endocostea* sp. from the Santonian-Campanian, Haslam Formation of Brannan Creek, Nanaimo District, British Columbia, Canada, demonstrate this point; in BM LL 28194 the inner 'rib' is poorly developed, starting at approximately 6 cm from the umbo of the right valve and continuing for only 2 cm, whereas BM LL 28217, a slightly smaller individual from the same locality and horizon, developed the rib at 1·5 cm from the umbo of the right valve, from which position it continues for at least 4·5 cm towards the posterior ventral margin.

In three well-preserved specimens from the late Campanian, Fort Pierre Group (two examples of '*Inoceramus*' aff. *barabini* Morton, BM L 21569 from the Cheyenne River Section, BM L 7577 from the Powder River Range, Montana, and a single example of '*Inoceramus*' *tenuirostris* Meek &

Hayden, 1862, BM L 21571, from the Cheyenne River), no fully developed internal rib is present. In its place are raised ridges on the innermost shell following the track of the normal position of the inner rib. These end distally as tangents to the 1 cm wide muscle scar that has been referred to as the posterior adductor. Clearly, inoceramids have an unusual arrangement of their soft parts, but it would appear the inner rib is formed as a sensitive emplacement of shell material to enhance strength in the part of the shell under stress from muscular shell closing.

The internal rib is also present on some Jurassic species; a well-preserved specimen of *Parainoceramus ventricosus* (J. de C. Sowerby, 1823) from the Lower Jurassic, Pliensbachian, at Brockthorpe, near Gloucester, shows precisely the same details as '*Inoceramus*' *barabini*, with an internal rib running down to the adductor. Some Campanian specimens of *Endocostea*, however, seem to show the internal rib running very close to the ventral margin, apparently past the position of the adductor.

There are also preservational problems in observing the internal rib. Early diagenesis of the aragonite shell interior can destroy the rib, and there are many examples of inoceramids preserved only as internal moulds of the outer calcitic shell layer.

The rib is nacreous, is often hollow and has an arch-shaped section. In all the examples that I have examined where two valves are preserved together, one rib is an almost perfect mirror image of the other. The rib is in a morphologically comparable position in all species in which it occurs. It shows distinct evolutionary changes, one of the most notable being extreme broadness in some species of *Seleniceramus* (Seitz 1967), though it is usually distinctly narrow. The internal rib may be close to a muscle scar at its distal end.

The claim that the internal rib is formed by, or in response to, a parasite may explain why it is sometimes filled with matrix. This can, however, be equally well explained if it is due to the activity of shell borers: if a hole is bored from the outside of the shell into the hollow of the rib, the damage cannot be repaired by deposition of more shell material as it is separated from the outer surface of the mantle by the thickness of the rib itself. The same would be the case if the inoceramid was already dead when its shell was drilled. All the cases of matrix- filled inner ribs that I have examined show evidence of drilling from the shell exterior.

The inner rib is clearly of some importance for taxonomy at both the species and higher levels. Its variability in some species and its possible diagenetic loss mean that it needs to be used with caution.

Genus *ENDOCOSTEA* Whitfield, 1877

TYPE SPECIES. *E. typica* Whitfield, 1877, by original designation. The lectotype (USNM 12261) was selected by Seitz (1967: 54–55, pl. 2, fig. 4). It is the example 'c' of Whitfield (1880: pl. 9 fig. 3) and is from the Pierre Shale at Old Woman Fork on the Cheyenne River, Black Hills, South Dakota, which is of late Campanian age according to Cobban & Reeside (1952: 1011) (*non Inoceramus cripsi* var. *typica* Zittel, 1866: 98, from the late Cretaceous of Grunbach in Neuen Welt and the Gosau Valley, Austria).

DISCUSSION. The generic name was introduced for relatively small inoceramids with a well-developed inner rib radiating from the umbo towards the posterior ventral margin but stopping well short of that margin. The species is otherwise very similar to Whitfield's own interpretation of *Inoceramus barabini* Morton (Whitfield, 1885: 75–76), except that the latter species apparently does not have the internal rib.

Subgenus *ENDOCOSTEA* Whitfield, 1877

A number of species or subspecies of *Endocostea* are rather convex with prominent or enrolled anterior umbones. These occur in the late Campanian and Maastrichtian and resemble *Endocostea (Endocostea) coxi* (Reyment). They include *Inoceramus balticus pteroides* (Giers, 1964: pl. 1, fig. 6) from the Upper Campanian, Polyplocum Zone of Haldem, Westfalia, and according to Sornay (1976) from Dau, Charente. They possibly also include *Inoceramus borilensis* Jolkicev, said to be from the Maastrichtian in Bulgaria. However, specimens that are very similar to *I. bakalovi* (said by Jolkicev (1961) to occur at the same horizon) occur with ammonites of the Upper Campanian, Donetzianum Horizon, in Nigeria. They also include *Inoceramus impressus* d'Orbigny (lectotype, Museum d'Histoire Naturelle, Paris, 7592a, figured Sornay, 1957: 129) from the ?Upper Campanian of Royan, and '*Inoceramus impressus*' d'Orbigny (*pars*, but not including the lectotype) from the Maastrichtian of Cotentin, Manche, France. These are provisionally included in the subgenus *Endocostea sensu stricto*, although their relationship with the less convex type species remains to be confirmed.

Endocostea (Endocostea) coxi (Reyment, 1958) Plate 1, figs 2–4

1958 *Inoceramus coxi* Reyment: 140, pl. 3, figs 4–6.

MATERIAL. The type material comes from Auchi in north-central Nigeria and is preserved in a medium grained, slightly ferrugenous sandstone (holotype BM L 82963). Some better preserved specimens occur on the Ikot Ekpene Road in the Calabar area associated with magnificent specimens of *Trochoceramus ianjonaensis* and are therefore of 'mid' (probably low Upper) Maastrichtian age. Another specimen in the BM(NH) collection comes from Madagascar. Three specimens were collected by Nolan and Skelton from the southwest face of Jebel Rawdah, BM LL 41647–49.

DESCRIPTION. Convex, equivalved species with strong radiating sulcus posterior to the umbones, delimiting a much less convex posterior area. Somewhat quadrate, but with umbones well to the anterior and prosocline. Strong radiating internal rib well to the posterior of the convex part of the shell. Strong but low rounded comarginal ribs, separated by wider interspaces on anterior and flank, ie. the convex part of the shell, fading posteriorly. Smoother in later growth stages.

COMMENTS. This species was included in *Cordiceramus* by Dhondt (1983a) following Seitz (1967), a genus that was included as a synonym of *Haenleinia* by Cox (1969). *Cordiceramus* Seitz (1961: 110, *ex.* Heinz, 1932) has a very distinctive wide external radiating furrow from the posterior of the umbo to the posterior ventral margin and is more or less equivalve. The type species, *C. cordiformis* Sowerby, is a relatively tall species with a short hinge line, whereas *Haenleinia* is an elongate genus related to *Endocostea*, with a posterior shell twist, resulting in an inequivalve shell in that
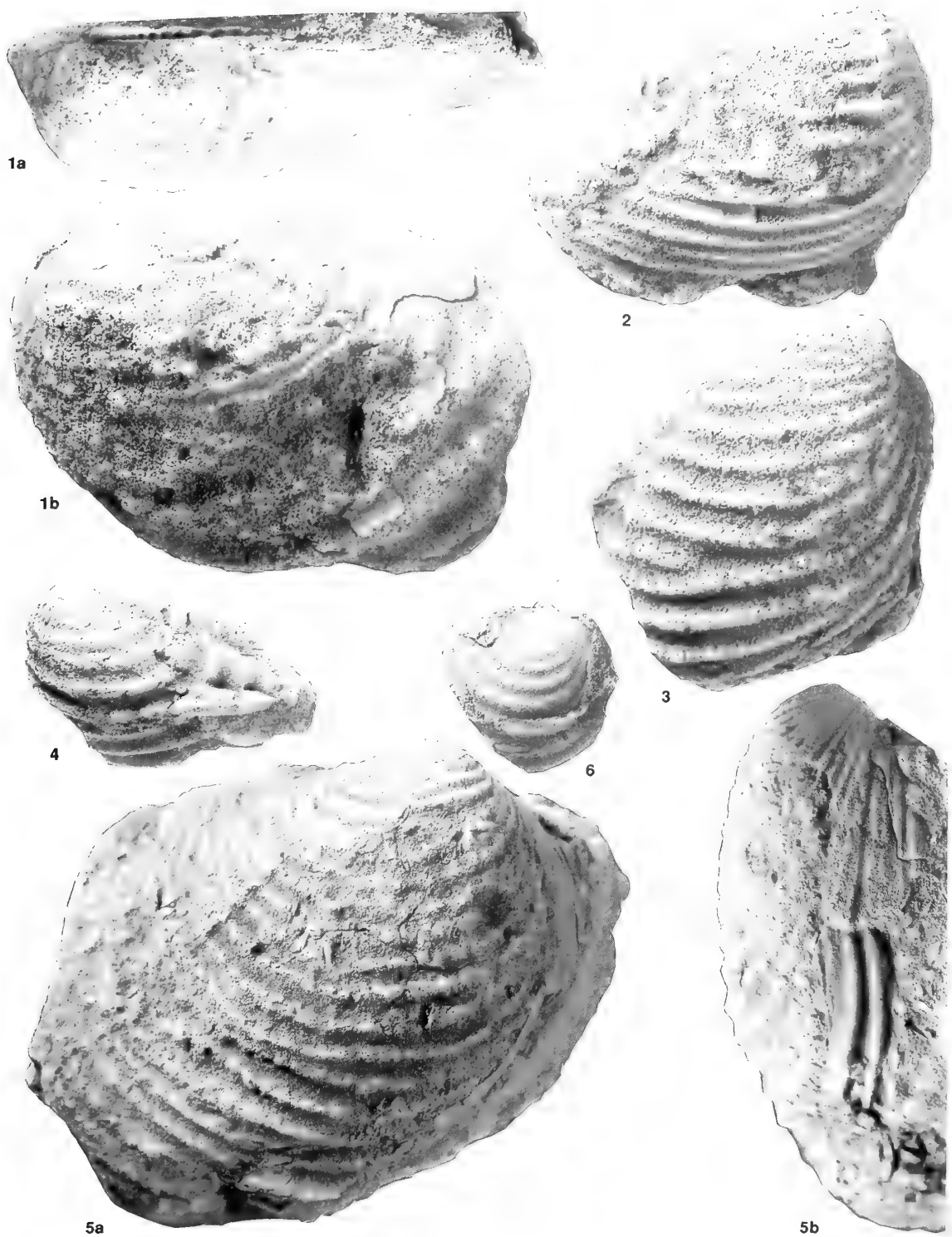
PLATE 1 Fig. 1   *Endocostea (Endocostea)* sp. indet.; BM LL 41651, left valve; south-west face of Jebel Rawdah, near base of Simsima
Formation, 'mid'-Maastrichtian; Skelton & Nolan Collection, × 2.

Figs 2–4   *Endocostea (Endocostea) coxi* (Reyment). **2**, BM LL 41647, **3**, BM LL 41648, both internal moulds of a right valves; **4**, BM LL
41649; internal mould of a left valve; all from the south-west face of Jebel Rawdah, Nolan and Skelton Collection, × 2.

Figs 5, 6   *Endocostea (Selenoceramus) semaili* sp. nov.; **5**, BM LL 41639, holotype, Jebel Rawdah, section 1, from scree below bed 5,
'mid'-Maastrichtian, Gale, Morris & Smith Collection, × 1; **6**, BM LL 41640, paratype, Jebel Rawdah, section 1, from bed 5,
'mid'-Maastrichtian, Gale, Morris & Smith Collection, × 2.

area. The radiating furrow in some specimens of *E. coxi* is found on composite moulds and reflects its internal rib. Well-preserved specimens of *E. coxi* from near Calabar, Nigeria, have no external furrow and do not seem properly placed in either *Cordiceramus* or *Haenleinia*.

Very similar specimens occur in the low Upper Maastrichtian part of the St Lucia Formation in South Africa (W.J. Kennedy, personal communication).

Endocostea (Endocostea) sp. indet.   Plate 1, fig. 1

1844   *Inoceramus impressus* d'Orbigny (pars): 515–16, pl. 409.

?1981   *Inoceramus (Endocostea) impressus* d'Orbigny; Tsankov *et al.*: 97, pl. 42, fig. 2.

MATERIAL. A single specimen from the south-western face of Jebel Rawdah, low in the Simsima formation, Skelton and Nolan Collection, BM LL 41651, 'mid'-Maastrichtian.

THE TYPE MATERIAL OF *INOCERAMUS IMPRESSUS*. Sornay (1957) chose the specimen from Royan in the d'Orbigny Collection as lectotype. This seems to have a much more prominent umbo than the present species, more closely resembling *E. borilensis* Jolkicev and *E. coxi* Reyment. The specimen here (Plate 1, fig 1) although not well preserved, is much more like the species from Cotentin that resembles the left valve only of d'Orbigny's figure. Specimens from the Maastrichtian of Cotentin in the de Gerville Collection in The Natural History Museum, resembling the right valve in d'Orbigny's figure, seem more closely related to *E. coxi* and are mentioned under *Endocostea (Endocostea)* above.

DESCRIPTION. Small elongate species with internal rib. Umbones well to the anterior but not prominent and incurled like the contempory species *E. coxi*. By means of this character, specimens from the Upper Maastrichtian of Cotentin are easily separable from *E. coxi*, although in d'Orbigny's description the species was described as inaequivalve. It seems that he considered that specimens with very prominent umbones, here thought to be related to *E. coxi*, were right valves of the species described here. The species also seems to occur commonly in the Maastrichtian rocks of the St. Lucia Formation from Zululand (W.J.Kennedy Collection).

Subgenus *SELENOCERAMUS* Seitz, 1967 (*ex*. Heinz, 1932)

TYPE SPECIES. *Inoceramus (Selenoceramus) selenae* Seitz, 1967, p. 95, by original designation.

Heinz's definition of *Selenoceramus* does not contain characters that distinguish this genus from others, except in his description of the two new species included in the genus. His type species, *Selenoceramus pulcher*, is treated by Seitz (1967: 94), somewhat dubiously, as a *nomen nudum*, apparently because there was no stated type specimen. Seitz attempted to validate the genus in terms of Heinz's original intention. Because of the ambiguity in ICZN article 13(a), it may prove necessary to apply to the International Commission to determine whether the genus should date from Heinz (1932) or Seitz (1967).

COMMENTS. *Selenoceramus* includes some rather small rounded inoceramids with concentric sculpture that show a marked change in growth direction following an evenly

curved young stage and have a wide internal rib. The material from the Omani Mountain area shows that this subgenus continues well into the Maastrichtian.

Endocostea (Selenoceramus) semaili sp. nov.   Plate 1, figs 5, 6

?1865   *Inoceramus cripsi* Mant, var. *regularis* d'Orbigny; Zittel: 93–99, pl. 14, fig. 3 only.

?1974   *Inoceramus regularis* d'Orbigny; Blank *et al*.: 85, pl. 21, fig. 2; pl. 23, fig. 1.

HOLOTYPE. BM LL 41639, from scree below bed 5, Simsima Formation, Maastrichtian; Jebel Rawdah, section 1; Gale, Morris and Smith Collection.

OTHER MATERIAL. Two small paratypes, BM LL 41640–41, from the same horizon and locality as the holotype; Gale Morris and Smith Collection. Three further paratypes, BM LL 41642–44, from the south-western outcrop in Jebel Rawdah, apparently from the same horizon; Nolan and Skelton Collection.

AGE. The accompanying ammonites and other species of Inoceramidae suggest that this species is of low Upper Maastrichtian age.

DESCRIPTION. Medium-sized inoceramids with close, regular, rounded, concentric ribs (which show a tendency to straighten) parallel to the anterior-ventral margin. Ribs approach dorsal margin at a relatively high angle to the posterior of the umbones. Maximum shell height below posterior point of hinge. Umbones orthocline, towards but not at anterior. Shells gently convex to a shell height of 70 mm in holotype, then a sharp change of direction to give increased width. This change of shell curvature is at variable distance from the umbones and occurs at an earlier growth stage in two of the paratypes.

The inner rib is angled at about 45° to the hinge line, and is only represented by a trace in the holotype. Two of the paratypes (LL 41642, 43) have a poorly preserved but distinctively wide and shallow internal rib, typical of the subgenus *Selenoceramus*.

The convexity and style of ribbing of *E. semaili* matches that of *E.* cf. *semaili* (Fig. 1) from the Lower Maastrichtian, *Acanthoscaphites tridens* Zone, at Nagoryani, Ukraine, except that it is smaller and the ribbing is consequently closer. However, approximately the same number of ribs are present. Unfortunately, specimens from Nagoryani are not well-preserved on the inner shell surface, making it very difficult to interpret the form of their interior ribs.

The species should be compared with *Endocostea mandembataensis* (Sornay, 1973: 90–91, pl. 4, fig. 4; Fig. 4) from Mandembata, southern Madagascar, 'Lower and Middle' Maastrichtian. Unfortunately, this species is defined on a single rather incomplete figured specimen. The anterior portion of the shell, a left valve, is missing, which does not allow identification at the species level. This species is a *nomen dubium* until further material from the type locality is described. Sornay himself (1973: 11) stated that the material was not sufficiently well preserved to enable him to work out its relationships.

Endocostea semaili should also be compared with *Endocostea kneri* Boehm (1909: 53; *nom. nov.* for *Inoceramus impressus* Kner, 1850, *non* d'Orbigny) from Nagoryani, Ukraine, presumably from the Lower Maastrichtian 'Tridens
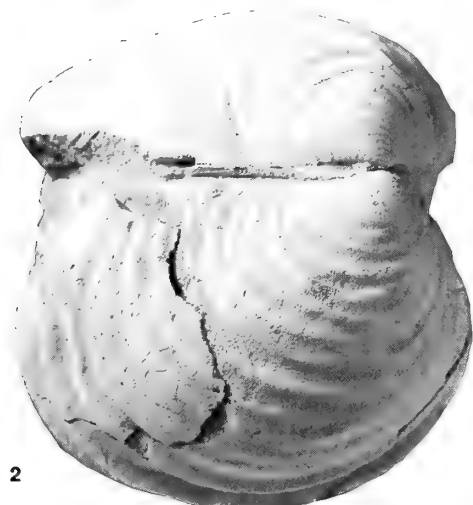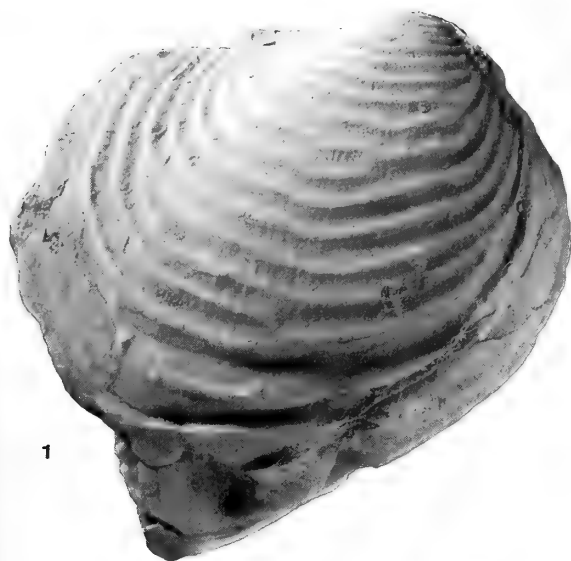
Fig. 1 *Endocostea (Selenoceramus)* cf. *semaili* sp. nov; 'Tridens' Zone, Lower Maastrichtian, Nagoryani, Ukraine; right valve; M. Mackay Collection, BM LL 41653, × 0·5.

Fig. 2 *Endocostea ?(Cataceramus)* sp. indet.; 'Tridens' Zone, Lower Maastrichtian, Nagoryani; M. Mackay Collection, BM LL 41654, × 0·5.

Zone'. When compared with sixteen specimens from Nagoryani in the collections of The Natural History Museum, it is fairly certain that the type of this nominal species is badly distorted. It has become much more elongated than all of them except one. The latter specimen, BM LL 61647, has a normal, rather rounded, right valve, but diagenetic distortion has decreased the height of the left valve. The similarity of the form of the sculpture of this left valve with that of Kner's figure suggests that his specimen was also similarly distorted. For this reason I consider that *Endocostea kneri* is a *nomen dubium* until such a time as its true shape can be described, possibly when the Inoceramidae from Nagoryani are revised. Specimens from Nagoryani are illustrated in Figs 1 and 2.

Endocostea semaili sp. nov. is very similar to *E. (Cataceramus) baltica* (Boehm, 1909; see Geirs, 1964: pl. 1, fig. 1 only)

from the late Santonian (? and Lower Campanian) of Germany, but it differs in having the umbones slightly more posterior. Also the comarginal ribs are much more regularly curved in Boehm's species, giving it a very rounded appearance, whereas there is a slight straightening of the ribs ventral to the umbones in *E. semaili*. The nature of the internal rib of *E. (Cataceramus) baltica* is in doubt.

Inoceramus sornayi Dhondt (1993) was a *nom. nov.* for *Inoceramus regularis* d'Orbigny, 1846, *non* Munster, 1840; the lectotype was designated by Sornay (1962), and other specimens were figured by him (Sornay, 1976: pl. 2, figs 3, 4; pl. 3, fig. 4). *I. sornayi* is from the late Campanian and has a wide internal rib, and like *Endocosta semaili*, is better placed in *Selenoceramus*.

E. (Selenoceramus) semaili has its umbones further from the anterior margin than *E. (S.) sornayi* and has a differently shaped anterior; its anterior ventral margin has a diagonally cut away appearance in contrast to the rounded anterior of *E. sornayi* (see Sornay, 1962: pl.7, fig. 3, the lectotype; and Dhondt, 1993: pl.6, fig. 3). *E. (S.) semaili* may have been a descendant and chronological subspecies of *E. (S.) sornayi*. It has not been found amongst the many Inoceramids in the St. Lucia Formation in South Africa, possibly because it is restricted to more northerly areas.

Subgenus *CATACERAMUS* Cox, 1969 (*ex*. Heinz, 1932 *?nom. nud.*)

TYPE SPECIES. *Inoceramus goldfussianus* d'Orbigny, 1845, by original designation.

Cox's designation of *Inoceramus goldfussianus* d'Orbigny as the type species is unfortunate because it is not the same as *I. balticus* Boehm as he claimed. More unfortunately, the specimen he figured as *I. balticus* has been separated from the type of that species by Giers, and is in fact the holotype of *I. marki* (Giers).

Heinz (1932: 15) proposed *Cataceramus*, with type species *Inoceramus balticus* Boehm, as a subgenus of *Selenoceramus*. Cox implied that Heinz's description does not fulfill the requirements of Article 13 (a) (i) in that there is no definition, and the name may therefore not be valid from that date. The type species, *I. balticus*, was emended by Giers (1964: 238–39). As pointed out by Dhondt (1993), Cox (1969) wrongly included *I. balticus* as a synonym of *I. goldfussianus*, and therefore changed the nature of the genus. Athough Heinz (1933) went on to use his generic name he still did not include characters that distinguished *Cataceramus* from other genera. Seitz (1967: 49) dismissed *Cataceramus* Heinz, 1932, as a synonym of *Endocostea* Whitfield.

IDENTITY OF THE TYPE SPECIES. *Inoceramus goldfussianus* d'Orbigny, 1845, was unnecessarily emended by Sornay (1957; 1976) to *I. goldfussi*. The species was described from the late Cretaceous of Royan by d'Orbigny, and he included the specimen figured by Goldfuss (1836: 116, pl. 112, fig. 4) as *Inoceramus cripsii* Mantell in his synonymy. Sornay (1957) figured the lectotype (d'Orbigny collection, no. 7593), previously chosen by Heinz, and also some new specimens (Sornay, 1976: pls 4, 5).

COMMENTS. In spite of the difficulties with the identity of the type species, this is the '*Inoceramus balticus*' group of many authors. Although Dhondt (1993) suggested that no close relative of *C. goldfussianus* can be recognised, both the

lectotype and Sornay's, 1976, pl. 4, fig. 2, have a definite indication of an internal rib in addition to a general similarity in shape to *I. balticus*. The clear difference is the more spaced out nature of the ribbing, which at present I regard as only significant at species level. *Endocostea (Cataceramus) goldfussianus* would seem to be of late Campanian age as understood here. Specimens from Celles near Riberac, Dordogne, France, suggest that the species occurs as early as the Vari Zone, Upper Campanian.

Upper Santonian and Lower Campanian species of *Cataceramus* are extensively described and illustrated by Seitz (1967) under the subgenus *Endocostea sensu stricto*. The inner rib of Seitz's *E. baltica baltica* is apparently intermediate in form between *Selenoceramus* and *Endocostea sensu stricto*. Unfortunately, the inner shell layer is not preserved on the lectotype of Böhm's species (Giers, 1964: pl. 1, fig. 2).

A number of additional species of this subgenus recognised in the Upper Campanian and Lower Maastrichtian are in need of further revision, but this is beyond the scope of the present paper. Two subspecies are, however, of stratigraphical value: *Endocostea baltica baltica* Boehm (1907: 113; 1909: pl. 11, fig. 2; emended Giers, 1964: 238–39, pl. 1, figs 2–4) and *E. baltica marki* occur in the Upper Santonian of Dulmen. Giers (1964), however, pointed out that *E. baltica* ranges higher, and he considered the subspecies *E. baltica haldemensis* (Giers 1964: 243–44, pl. 2, fig. 2) from the Polyplocum Zone of Haldem, Lemforde, Westfalia (?*non Inoceramus haldemensis* Heinz, ?*nomen nudum*) to be typical of the Upper Campanian. Two other subspecies, *E. baltica ellipticus* and *E. baltica sublaevigatus*, occur in the low Upper Campanian at Tercis, south-west France (Dhondt, 1993).

Endocostea (?Cataceramus) **aff.** *goldfussianus*
(d'Orbigny, 1846)   Plate 2, fig. 4

1846   *Inoceramus goldfussianus* d'Orbigny: 517, pl. 411.
1976   *Inoceramus goldfussi* d'Orbigny; Sornay: 9–11, pl. 4; pl. 5, figs 4, 5.

MATERIAL. A single specimen, kindly donated by Mrs Valerie Chalmers and other members of the UAE Natural History Group, BM LL 41645. Apparently from Jebel Rawdah, its calcarenite matrix is rich in *Lepidorbitolina* sp., and it seems to come from the same horizon as the other material from this locality.

COMMENTS. Whereas this individual might be a variant of *E. (S.) semaili* sp. nov., it has a rather different ribbing pattern, clearly similar to that of the earlier *E. golfussianus* (d'Orbigny), but closer packed. There is a slight change in shell curvature suggesting that it would have been a considerably smaller individual when full grown than the typical late Campanian specimens of western France. It also closely resembles a specimen from the Lower Maastrichtian, 'Tridens Zone', of Nagoryani, Ukraine (Fig. 2).

ENDOCOSTEA BEBAHOAENSIS AND RELATED SPECIES. A number of inflated species of late Campanian and Maastrichtian age seem to form a natural group. They have umbones well to the anterior and show no change of growth direction as they approach full size. They include:

1. *Inoceramus cripsi* Mantell var. *decipiens* Zittel, 1865: 95–99, pl. 15, fig. 1; Gosau Beds, Grunbach, Austria.
2. *Inoceramus bebahoaensis* Sornay, 1973: 89, 90, pl. 3, figs 1, 2, text–fig. 4.
3. *Inoceramus balticus beckumensis* Giers, 1964: pl. 2, fig. 1, from the low Upper Campanian, Beckumer Schichten, near Beckum, Germany.
4. ?*Inoceramus balticus* Boehm, Blank *et al.* 1974: 83, pl. 22, fig. 2.
5. *Inoceramus borilensis dauensis* Sornay, 1976: 5, 6, pl. 1, fig. 3; pl. 2, figs 1, 2.
6. *Endocostea flexibaltica* (Seitz); Dhondt, 1993: pl. 4, fig. 4.
7. ?*Inoceramus borilensis* Jolkicev, 1962: 145, pl. 7.

There is apparently no subgeneric name for this group, but I consider it inadvisable to introduce one here because the full relationships within *Endocostea* are insufficiently understood.

'Endocostea' bebahoaensis (Sornay, 1973)   Plate 2, figs 1, 2

1973   *Inoceramus bebahoaensis* Sornay: 89–90, pl. 3, figs 1–2, Fig. 4.

MATERIAL. A single well-preserved specimen from the south–west face of Jebel Rawdah, Nolan and Skelton Collection, BM LL 61646.

MATERIAL FROM OTHER LOCALITIES. A single specimen, BM L 74737, from the Upper Maastrichtian, Calcaire a *Baculites*, Cotentin Peninsula, Normandy, in the de Gerville (ex J. de C. Sowerby) Collection. Other specimens are known from the Maastrichtian of Ianjona and Bebahoa, southern Madagascar (Sornay, 1973), and the St. Lucia Formation, Zululand (W.J.Kennedy Collection, Oxford University Museum).

DESCRIPTION. Convex medium-sized species of Inoceramidae with unchanging growth curvature and only gently coarsening, regular, low, rounded, concentric ribs. Umbones well to the anterior and gently prosocline. Our single right valve from Jebel Rawdah is an internal mould and has a shallow narrow groove running from the umbo towards the posterior ventral margin as far as the shell is preserved. This is the impression of the internal rib, which does not seem to have been preserved on other specimens.

PLATE 2

Figs 1, 2 '*Endocostea*' *bebahoaensis* (Sornay). **1**, BM L 74737, Calcaire à *Baculites*, Upper Maastrichtian, Cotentin Peninsula, France, de Gerville Collection; left valve, 1a, anterior view, 1b, lateral view, × 1. **2**, BM LL 41646, south-west face of Jebel Rawdah, 'mid'-Maastrichtian, near base of Simsima Formation; Nolan & Skelton Collection; right valve, 2a, lateral view, 2b, anterior view, 2c, dorsal view; × 1.

Fig 3 '*Endocostea*' cf. *bebahoaensis* (Sornay). BM LL 41652, *Loftusia*-Beds, Jebel Huwayyah, ?Early Maastrichtian, Gale, Morris & Smith Collection, anterior view of incomplete right valve, × 1.

Fig. 4 *Endocostea (?Cataceramus)* aff. *goldfussianus* d'Orbigny. BM LL 41645, possibly from near the base of the Simsima Formation, Jebel Rawdah. ?Maastrichtian, Mrs. V. Chalmers Collection; 4a, lateral view of right valve, 4b, anterior view, × 1.

'Endocostea' cf. *bebahoaensis* (Sornay, 1973). Plate 2, fig. 3

cf. 1973 *Inoceramus bebahoaensis* Sornay: 89–90, pl. 3, figs 1–2, Fig. 4.

MATERIAL AND COMMENTS. A single fragment, BM 41652, from the *Loftusia*-Beds at Jebel Huwayyah, consists of only the anterior portion of the shell. The anterior position of the umbo, the steep drop from the convex flank to the anterior margin and the style of ribbing, demonstrate that this fragment is very similar to *Endocostea bebahoaensis*, particularly the specimen from Cotentin (Plate 2, fig. 1). Ammonite evidence suggests that the Campanian-Maastrictian boundary may lie within the *Loftusia*-Beds, and the occurrence of *Pachydiscus dossantoi* (Maury, 1930) in the upper part of these beds suggests that the age here is at least as high as mid-Maastrichtian.

Genus *PLATYCERAMUS* Seitz, 1961, p. 54
(*ex. Platyceramus* Heinz, 1932, p. 10, *nomen nudum*)

TYPE SPECIES. *Inoceramus mantelli* de Mercy, 1877, by original designation.

As originally introduced by Heinz (1932: 10), with the type species designated as 'Genotyp: *Inoceramus mantelli* Merc.', it is difficult to interpret this generic name as anything but a *nomen nudum*, because no description or differentiating characters were given. *Inoceramus mantelli* de Mercy, 1877, is based on a number of hinge and outer shell fragments of large inoceramids from northern France, ranging in age from Turonian to Coniacian and possibly into the Lower Santonian. Many of these fragments are similar to bilaterally symmetrical species of immense proportions, not uncommon in the Chalk of England and northern France, but are otherwise not particularly different from *Inoceramus cuvieri* Parkinson, 1819. On this basis it does not therefore seem necessary to distinguish *Platyceramus* from *Inoceramus sensu stricto*.

In Seitz's (1961: 54) more valid use of *Platyceramus* (as a subgenus of *Inoceramus*), the type species *Inoceramus mantelli* de Mercy, 1877, was interpreted according to Barrois' (1879) description of the species (which was based on ?Coniacian specimens). Barrois' interpretation of *I. mantelli* differs from *I. cuvieri* in having a very much wider umbonal angle, in which respect it resembles the South African Coniacian species *'I'* *expansus* Baily. It will be necessary to apply to the I.C.Z.N. if this interpretation of *Platyceramus* and its type species is to be accepted.

Seitz had a wide interpretation of the genus and included many flattish, bilaterally symmetrical inoceramids from varying parts of the Upper Cretaceous, eg. *Inoceramus cycloides* Wegner. Similar large, often smoothish, narrow species also occur in the Campanian and Maastrichtian. It is difficult to believe that all these flattish species are correctly assigned to the same clade and some will need different generic names. No attempt to solve this taxonomic problem is attempted here.

Cf. *Platyceramus* sp. indet.

MATERIAL. A single fragmentary specimen of an almost smooth, very large species was observed in the main gastropod bed at the base of the Simsima Formation at Jebel Bu

Milh, section 2. It showed no other characters. The specimen was not collected, but it indicates the presence of *'Platyceramus'*. This genus is common in the Lower Maastrichtian part of the St. Lucia Formation, South Africa, and although less common in the Upper Maastrichtian part of that formation, the highest *Inoceramus* horizon seems to consist entirely of fragments belonging to *'Platyceramus'*.

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Late Campanian-Maastrichtian Bryozoa from the United Arab Emirates-Oman border region

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SYNOPSIS. Seven species of bryozoans have been found encrusting cobbles from the Qahlah Formation (Upper Campanian or Maastrichtian) of Jebel Huwayyah, east of Al Ain, UAE. This preliminary report describes and figures the Jebel Huwayyah bryozoan fauna and draws attention to its importance as a rare example of a bryozoan fauna from the Cretaceous tropics. The following taxa are described: *Bullaconopeum nodosum* gen. et sp. nov., *Biaviculigera* sp., *Pelmatopora* sp., *Leptocheilopora* sp., *Tecatia* sp., *Voigtopora* sp. and '*Berenicea*' sp.

INTRODUCTION

Bryozoans are sessile, suspension-feeding, colonial inverte-brates, predominantly marine and typically with fossilizable skeletons of calcite. They often form a major component of Upper Cretaceous marine biotas: in north-west Europe indi-vidual assemblages sometimes contain a hundred or more species (e.g. Voigt 1973; Taylor 1987). Cretaceous bryozoans from other parts of the world are much less well-known and appear to be relatively low in both diversity and abundance. Nevertheless, Upper Cretaceous faunas have been found in regions as far apart as North America, India and Western Australia. However, bryozoans of this age have yet to be described from the Arabian Peninsula.

This paper is a preliminary description of a well-preserved fauna of encrusting bryozoans from the Qahlah Formation (Nolan *et al.* 1990; Skelton *et al.* 1990) of the Oman Moun-tains. The Qahlah Formation is late Campanian or early Maastrichtian in age (A. B. Smith *et al*, this volume). In the Jebel Huwayyah area it is thought to represent a transgressive fan delta depositional system (Skelton *et al.* 1990). The bryozoans were collected from Bed 7 of A. B. Smith *et al.* (this volume, Fig. 8) where they encrust cobbles together with the oyster *Acutostrea* and colonial corals. Although Smith *et al.* interpreted this bed as a shoreface facies, the moderately high diversity and general composition of the bryozoan fauna (with only one malacostegan) suggests a subtidal origin.

The seven bryozoan taxa found in the Qahlah Formation extend the geographical ranges of some genera formerly unrecorded in the Middle East. The bryozoans have particu-lar significance in providing a rare glimpse of a tropical Cretaceous bryozoan fauna which can be compared with the temperate to subtropical faunas found elsewhere, notably in north-west Europe. Six of the seven species are identified to genus level only, pending further study and availability of additional material. The seventh species is distinctive and is represented by sufficient material to warrant its description as a new genus and species.

SYSTEMATIC PALAEONTOLOGY

All of the material is from the Qahlah Formation (Upper Campanian or Maastrichtian), Bed 7, SE corner of Jebel Huwayyah 1 (see A. B. Smith *et al.*, this volume), east of Al Ain, UAE/Oman borders (Sheet NG–40–14D; 1:100,000 grid reference CM 842878). Specimens are registered in the collections of The Natural History Museum, London. Scan-ning electron micrographs were prepared from uncoated specimens, imaged using back-scattered electrons (see Taylor 1986).

Cheilostome classification used here follows Gordon (1989), although it is recognized that analysis of phylogenetic relationships must precede a more satisfactory scheme.

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Order **CHEILOSTOMIDA** Busk, 1852
Suborder **MALACOSTEGINA** Levinsen, 1902
Superfamily **MEMBRANIPOROIDEA** Busk, 1854
Family **ELECTRIDAE** Stach, 1937
Genus *BULLACONOPEUM* nov.

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TYPE SPECIES. *Bullaconopeum nodosum* sp. nov.; Upper Cretaceous, Qahlah Formation, Oman Mountains.

NAME. Combination of *bulla* (Latin, knob, in reference to the tubercles) with the established bryozoan genus *Conopeum* (Latin, mosquito net).

DIAGNOSIS. Colony encrusting, multiserial; autozooidal ope-sia ovoidal, distal part smooth and crescent-shaped; crypto-cyst pustulose, broad proximally, moderately broad laterally but absent distally; gymnocyst narrow, occasionally more extensive proximally; four gymnocystal tubercles present, two located near proximo-lateral corners of cryptocyst, two at distal edges of cryptocyst where crescent-shaped distal part of opesia begins; kenozooids occasionally developed, irregular in shape, with pustulose cryptocyst surrounding entire opesia, lacking the crescent-shaped smooth distal area of autozooids; pore chambers apparently lacking; intramural buds present, closure plates not observed; ovicells and avicularia not seen, presumed absent; early astogeny unknown.

REMARKS. This new monospecific genus is distinguished by the presence of four blunt tubercles around the edges of the autozooidal cryptocyst. The crescentic shape of the distalmost part of the opesia arching between the two disto-lateral tubercles is also characteristic and is presumably more-or-less coincident with the location of the orifice and operculum in the living zooid. The absence of ovicells supports assignment of *Bullaconopeum* to the malacostegans, a paraphyletic grade of primitive cheilostomes which at the present day have non-brooded planktotrophic larvae (cyphonautes). This is corroborated by the fact that avicularia are also lacking, even in areas of zooidal crowding where they might be expected to be found but where kenozooids are developed instead. Among malacostegan genera, *Bullaconopeum* resembles *Eokotosokum* Taylor & Cuffey, 1992, from the Maastrichtian of Alberta. This Canadian genus shows a similar development of the cryptocyst but has two large disto-lateral spine bases and no tubercles. Several other malacostegan genera (e.g. *Charixa*, *Spinicharixa*, *Villacharixa*; see Taylor & Cuffey 1992) possess spine bases which are lacking in *Bullaconopeum*, although it is possible that the tubercles of *Bullaconopeum* represent an evolutionary development from articulated spines. Tubercles occur in some malacostegan and other cheilostome genera. Voigt (1992) observed that they were especially common in bryozoans living in high energy environments (e.g. on algal fronds), were often variably present, and suggested that they may function in preventing mechanical damage. In contrast, the tubercles of *Bullaconopeum* are always present and occur in colonies living in protected microhabitats such as burrows.

Two families of malacostegans are recognized: Electridae and Membraniporidae. *Bullaconopeum* is provisionally assigned to the former family, which is much more diverse, but confident placement must await the discovery of early astogenetic stages to ascertain whether the ancestrula is simple (Electridae) or twinned (Membraniporidae).

Bullaconopeum nodosum sp. nov.   Pl. 1

HOLOTYPE. BMNH BZ 3167.

PARATYPES. BMHN BZ 3168 (1), 3172 (1), 3173.

NAME. From *nodus* (Latin, knot), in reference to the node-like tubercles.

DESCRIPTION. Colonies are encrusting and sheet-like (Pl. 1, fig. 1), attaining a maximum diameter of at least 25 mm. None of the available specimens show unequivocal early astogenetic stages and therefore nothing is known of the ancestrula or early budding pattern. Abraded parts of colonies (Pl. 1, fig. 6) show that the basal wall of the zooids are fully calcified but that pore chambers are lacking.

Autozooids have a rounded rhomboidal shape and are relatively broad (Pl. 1, figs 2–3). In the holotype frontal length of the autozooids averages 0·38 mm (range = 0·32–0·47 mm; n = 15) and frontal width 0·35 mm (range =

0·27–0·39 mm; n = 15). An elongate ovoidal opesia occupies much of the frontal area of the autozooid. Opesial length in the holotype averages 0·27 m (range = 0·24–0·30 mm; n = 15) and opesial width 0·19 mm (range = 0·17–0·21 mm; n = 15). Cryptocyst borders the opesia proximally and laterally, whereas gymnocyst, slightly raised to form a distinctive semi-circular crescent, defines the distalmost edge of the opesia. The cryptocyst is pustulose, and is widest and shelf-like proximally but narrows and slopes more steeply inwards along the lateral edges of the opesia. The perimeter of the cryptocyst is slightly depressed relative to the surrounding gymnocyst, and the cryptocyst:gymnocyst boundary is well-defined and minutely beaded. The smoothly calcified gymnocyst forming the outer edge of the autozooid is narrow, especially laterally. Four conspicuous but short tubercles occur along the inner edge of the gymnocyst. Tubercle diameter is about 40–50 µm. The proximo-lateral pair of tubercles are located approximately level with, or a little proximally of, the proximal edge of the opesia. They mark the transition from the proximal gymnocyst to the narrower lateral gymnocyst. The disto-lateral pair of tubercles are situated where the pustulose cryptocyst ends and is replaced by gymnocyst forming the characteristic crescent-shaped distal edge of the opesia. Closure plates have not been observed, although some zooids are plugged with sediment which bears a superficial resemblance to a closure plate. Intramural buds are developed in some autozooids as an additional rim of cryptocyst within the opesia (Pl. 1, fig. 5).

Kenozooids are present sporadically (Pl. 1, fig. 4). They are slightly smaller than the autozooids and more irregularly shaped. Tubercles are lacking, the opesia is reduced relative to that of an autozooid, and cryptocyst surrounds the entire opesia, unlike autozooids where it is absent distally.

Ovicells and avicularia have not been found and are presumed to be absent.

REMARKS. *Bullaconopeum nodosum* is the most conspicuous and commonest of the bryozoans encrusting the collection of cobbles from Jebel Huwayyah. Colonies occur within pre-cementation burrows as well as on cobble surfaces where they are less well-preserved. Colony-form and zooid dimensions resemble those found in *Biaviculigera* sp. This similarity is readily appreciated as superficial when the two species are studied using SEM (compare Pl. 1, fig. 2 with Pl. 2, fig. 1).

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Suborder **NEOCHEILOSTOMINA** d'Hondt, 1985
Infraorder **PSEUDOMALACOSTEGOMORPHA** d'Hondt, 1977
Family **CALLOPORIDAE** Norman, 1903
Genus *BIAVICULIGERA* Voigt, 1989

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Biaviculigera sp.   Pl. 2, fig. 1

MATERIAL. BZ 3171.

REMARKS. A well-preserved specimen of an unidentified

PLATE 1

Figs 1–6 *Bullaconopeum nodosum* gen. et sp. nov., Qahlah Formation (Upper Campanian or Maastrichtian), Bed 7 of Smith *et al.* (this volume), SE corner of Jebel Huwayyah 1, east of Al Ain, UAE/Oman borders. **1–4**, BMNH BZ 3167, **holotype**; **1**, multiserial arrangement of zooids, × 35; **2**, group of autozooids showing tubercles and pustulose cryptocysts, × 90; **3**, autozooid with sediment-filled opesiae, × 150; **4**, kenozooid partly filled by sediment, × 120. **5–6**, BMNH BZ 3168 (1); **5**, autozooid (? astogenetically early) at preserved lateral edge of colony showing proximo-lateral pore window (right of centre) and intramural bud, × 150; **6**, abraded growing edge exposing calcified basal walls of zooids and vertical walls seemingly lacking pore chambers, × 90.

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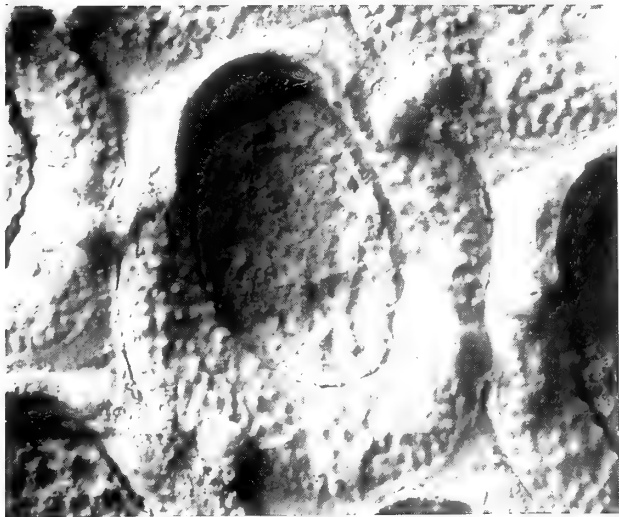
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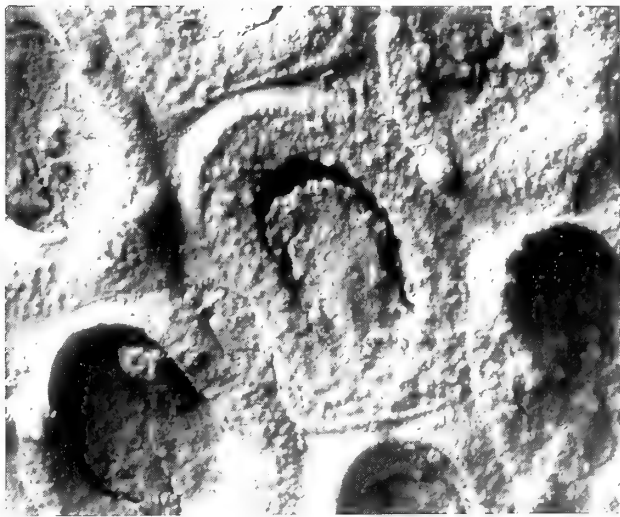
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species of *Biaviculigera* has a sheet-like encrusting colony with spineless autozooids, non-pustulose cryptocysts, avicularia and ovicells. This genus (type species *Membranipora praecipua* Brydone, 1914) was proposed by Voigt (1989) for nine species of Cenomanian-Maastrichtian cheilostomes, seven of which were formerly assigned to the genus *Membranipora* as used in its broadest sense. *Biaviculigera* is characterized by having two types of avicularia. In the Qahlah Formation species these comprise large avicularia with spatulate rostra and small avicularia with pointed rostra.

Suborder **ASCHOPHORINA** Levinsen, 1909
Infraorder **CRIBRIOMORPHA** Lang, 1916
Family **PELMATOPORIDAE** Lang, 1916
Genus *PELMATOPORA* Lang, 1916

Pelmatopora sp.   Pl. 2, fig. 2

MATERIAL. BZ 3170.

REMARKS. *Pelmatopora* is a diverse genus which ranges from the Coniacian to the Upper Campanian or possibly Danian (Larwood 1962). The Qahlah Formation species has about 16–20 arched costae, each with a large pelma (pore) in the narrow median area of costal fusion. Pelmatidia and lateral costal fusions seem to be absent, and 'interzooecial secondary tissue' (sensu Larwood 1962) and oral spines have not been observed. However, sediment obscures much of the morphological detail. A few zooids bear ovicells, and many have small paired avicularia located on either side of the high autozooidal orifice, inwardly directed towards the orifice, spatulate and with well-developed transverse bars.

Genus *LEPTOCHEILOPORA* Lang, 1916

Leptocheilopora sp.   Pl. 2, fig. 3

MATERIAL. BZ 3169 (3).

REMARKS. An inconspicuous colony of *Leptocheilopora* encrusts one of the cobbles. The small autozooids have about 14–16 closely-spaced costae forming a flat frontal shield. Four oral spines are present and there are numerous small avicularia, each with a relatively large proximal gymnocyst and a spatulate rostrum without a transverse bar. Lateral costal fusions and pelmata have not been observed. The orifice has well marked lateral constrictions, dividing a deep poster from the distal anter. None of the species of *Leptocheilopora* revised by Larwood (1962) compares closely with the Qahlah Formation species, especially with regard to the avicularia which are uncommon in this genus. In Europe *Leptocheilopora* ranges from the Santonian to the Maastrichtian (Larwood 1962).

Infraorder **HIPPOTHOOMORPHA** Gordon, 1989
Family **HIPPOTHOIDAE** Fischer, 1866
Genus *TECATIA* Morris, 1980

Tecatia sp.   Pl. 2, fig. 4

MATERIAL. BZ 3168 (2).

REMARKS. The tiny autozooids of this ascophoran are dispersed widely across the substratum, and arranged in a seemingly chaotic manner. It is unclear whether the wide-spacing of the autozooids is because they have long caudae, are interspersed with stolon-like heterozooids, or reflects loss of intervening zooids. The autozooidal orifice has a distinct sinus, and the strongly arched gymnocystal frontal wall shows a line of pore windows just above substratum level. Although this species is assigned to *Tecatia*, the minute pores in the frontal wall which are characteristic of *Tecatia* have not been observed, possibly because of preservational limitations.

Tecatia is represented by four species from the Upper Maastrichtian of the type area and one Recent species from the Pacific coast of North and Central America (Morris 1980; Voigt & Hillmer 1983). Voigt (1987) described how *T. minuta* Morris, 1980, can be found in 'minicaverns' formed by thalassinoid burrows in hardgrounds in the Maastrichtian Chalk Tuff. Similarly, the Qahlah Formation species of *Tecatia* inhabited the cryptic habitats provided by precementational burrow systems in cobbles.

Order **CYCLOSTOMATA** Busk, 1852
Suborder **TUBULIPORINA** Milne Edwards, 1838
Family **STOMATOPORIDAE** Pergens & Meunier, 1886
Genus *VOIGTOPORA* Bassler, 1952

Voigtopora sp.   Pl. 2, fig. 5

MATERIAL. BZ 3169 (1), 3172 (2).

REMARKS. A few colonies of the runner-like cyclostome *Voigtopora* encrust the cobbles. This genus is distinguished from the related *Stomatopora* by the presence of lateral branch ramifications and the long proximal extensions of the zooids which flank the previous zooid in linear series (see Illies 1976). *Voigtopora* appears to range from the Hauterivian to the Campanian in Europe (Pitt & Taylor 1990), and also occurs in the Albian and Cenomanian of Texas. The species-level systematics of this genus is in need of revision, with characters of early colony development likely to be of considerable importance.

PLATE 2

Figs 1–6   Bryozoans from the Qahlah Formation (Upper Campanian or Maastrichtian), Bed 7 of Smith *et al*. (this volume), SE corner of Jebel Huwayyah 1, east of Al Ain, UAE/Oman borders; **1,** *Biaviculigera* sp., BMNH BZ 3171, part of colony showing autozooids with smooth cryptocysts, a large spatulate avicularium (in recess, centre left), and several small acuminate avicularia, × 60; **2,** *Pelmatopora* sp., BMNH BZ 3170, autozooid (partly obscured by sediment) showing large pelmata in median area of costal fusion, × 100; **3,** *Leptocheilopora* sp., BMNH BZ 3169 (3), autozooid flanked by two small, abraded avicularia, × 230; **4,** *Tecatia* sp., BMNH BZ 3168 (2), oblique view of a zooid with sediment-plugged orifice (arrow) and line of basal pore windows, × 250; **5,** *Voigtopora* sp., BMNH BZ 3169 (1), branch with three zooids viewed obliquely, × 45; **6,** '*Berenicea*' sp., BMNH BZ 3169 (2), part of colony showing transversely-wrinkled frontal walls, × 45.

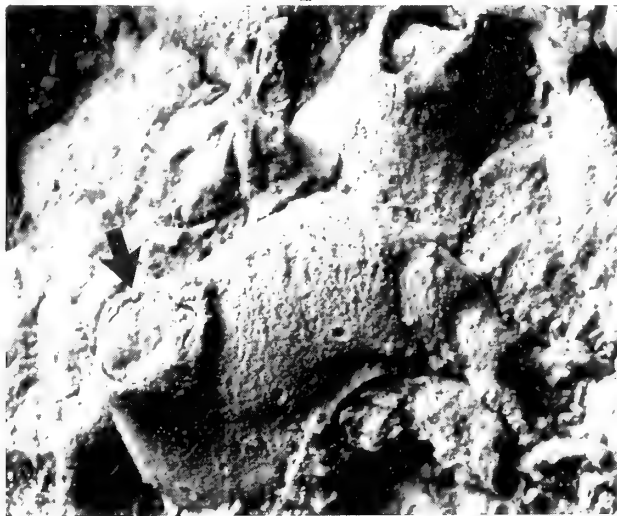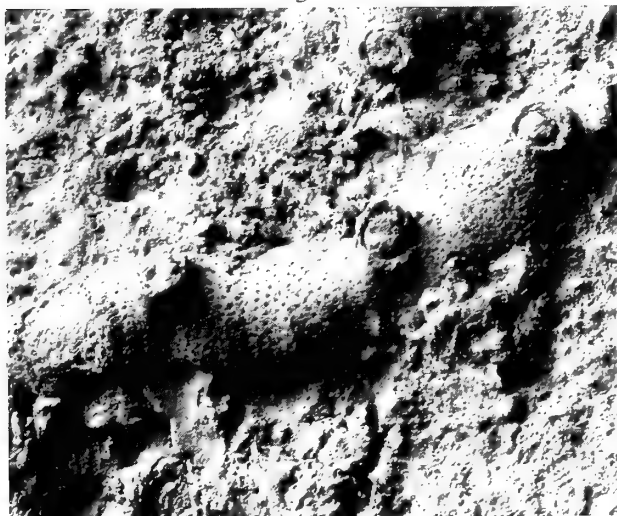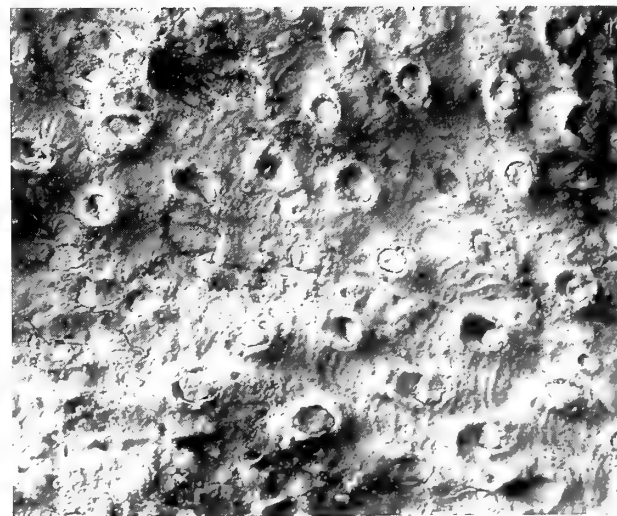Family **incertae sedis**
Genus '*BERENICEA*' Lamouroux, 1821

'*Berenicea*' sp.   Pl. 2, fig. 6

MATERIAL. BZ 3169 (2).

REMARKS. Part of a sheet-like tubuliporine cyclostome is
present at the edge of one of the burrows. The zooidal frontal
walls are transversely wrinkled, but in the absence of gono-
zooids it is impossible to assign the colony to a genus.
Therefore, following the procedure adopted by Taylor &
Sequieros (1982) and Pitt & Taylor (1990), the specimen is
placed in the informal genus '*Berenicea*'.

DISCUSSION

This new bryozoan fauna has both palaeobiogeographical and
palaeoecological importance. As noted above, the great
majority of Cretaceous bryozoan faunas have been described
from Europe. Nothing was previously known of Upper
Cretaceous bryozoan faunas from the Arabian Peninsula.
The Qahlah Formation specimens therefore fill a major
geographical gap in our knowledge of Upper Cretaceous
bryozoans. Furthermore, as the late Cretaceous proto-Oman
Mountains would have been located almost on the palaeo-
equator (e.g. A. G. Smith *et al.* 1994), it provides a tropical
fauna that can be compared with the temperate faunas of
Europe and elsewhere. Six of the seven genera found in the
Qahlah Formation occur also in north-west Europe, the
exception being *Bullaconopeum*. At the genus-level, there-
fore, it is seems that there was little taxonomic differentiation
between late Cretaceous temperate and tropical bryofaunas.
In addition, albeit based on a small number of species, the
proportion of cheilostomes (five species) to cyclostomes (two
species) in the tropical Qahlah Formation is fairly typical for
a fauna of this age (cf. Lidgard *et al.* 1993, fig. 7).

Along with other cemented invertebrates and plants, bryo-
zoans are commonly found encrusting the surfaces of cobbles
like those from the Qahlah Formation. Cobbles provide a
variety of different microhabitats for these sessile organisms,
including upper and lower external surfaces, and crevices
formed by vacated borings or pre-cementational burrows.
Therefore, cobbles allow the study of small scale niche
differentiation among demonstrably in-situ organisms. Few
studies of cobble-dwellers have been undertaken in the fossil
record, and the only detailed study involving a diverse
Cretaceous bryozoan fauna is that of Wilson (1986) on
cobbles from the Aptian Faringdon Sponge Gravel of
England. Wilson found a clear distinction between species
colonizing the outer surfaces of the cobbles, which were
robust in morphology, and species living in vacated borings,
which often had a delicate construction. This he interpreted
as a consequence of the physical rigours experienced by the
encrusters on outer surfaces compared with the protected
burrows. Preliminary study suggests that a similar differentia-
tion may occur among the colonizers of the Qahlah Forma-
tion cobbles, although further field sampling and careful
mapping of distributions will be needed to substantiate this
impression. It would be particularly instructive to compare
the cyclostome-dominated Aptian Faringdon Sponge Gravel

cobbles with the cheilostome-dominated younger Qahlah
Formation cobbles.

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Maastrichtian brachiopods from the United Arab Emirates-Oman border region

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INTRODUCTION

Brachiopods were particularly rare in the Maastrichtian sediments of the United Arab Emirates-Oman borders region. Despite intensive collecting only four specimens were found, all coming from the lower *Loftusia*-rich beds of the Qahlah Formation exposed at Jebel Huwayyah (see introduction for locality details). These four specimens belong to a hitherto undescribed genus of terebratulid.

SYSTEMATIC DESCRIPTIONS

Class **TEREBRATULIDA** Waagen, 1883
Suborder **TEREBRATULIDINA** Waagen, 1883
Superfamily **TEREBRATULACEA** Gray, 1840
Family **TEREBRATULIDAE** Gray, 1840
Genus *PSEUDOGIBBITHYRIS* nov.

TYPE SPECIES. *Pseudogibbithyris arabica* sp. nov.

DIAGNOSIS. Medium-sized uniplicate terebratulid, slightly longer than wide. elongate-oval in general outline and evenly biconvex. Umbo short, beak suberect, foraman small, permesothyrid. Cardinal process present, brachial loop simple.

REMARKS. *Pseudogibbithyris* differs from *Gibbithyris* and *Concinnithyris* from the European Upper Chalk (Senonian), which it resembles in external morphological features, in its

Fig. 1. *Pseudogibbithyris arabica* gen. et sp. nov., holotype, BMNH BF47; Jebel Huwayyah, section 2, beds 3–6. A, dorsal; B, lateral; C, anterior views: all × 1.

distinctly flat bifid cardinal process, deep hinge-trough and short, triangular hinge-plates.

Pseudogibbithyris arabica sp. nov.   Figs 1, 2

DIAGNOSIS. As for genus.

TYPES. Holotype, BMNH BF47; paratypes BMNH BF44–46.

DESCRIPTION. The dorsal valve is dominated by a low median fold bounded by faint carinae originating from a point midway between the umbonal area of the valve and the anterior margin of the shell. A corresponding shallow sulcus in the ventral valve forms a wide, shallow uniplication occupying the whole width of the anterior commissure.

Internal characters include a well-developed flat, but distinctly bifid cardinal process, and a deep hinge-trough. The hinge-plates are short, triangular in outline with a slightly concave ventral surface, and are deflected towards the dorsal valve. The triangular shape of the hinge-plates is maintained in the development of the horizontally placed bands of the descending branches of the brachial loop, which is uncomplicated and terminates in a very high arcuate transverse band.

REMARKS. The only morphological features which this species has in common with other Terebratulidae of the Upper Cretaceous are the distinctly oval general outline and uniplicate anterior commissure. The internal structure, notably the distinctive cardinalia and short triangular hinge-plates, are features more typical of terebratulid species of the Upper Jurassic to Lower Cretaceous, the closest comparison being to species of *Nucleata* and *Pygites*. However, it is not suggested that there is any direct relationship between the species described here as *Pseudogibbithyris arabica* gen. et sp. nov. and the Tithonian genera mentioned above. As no reference to any forms which could be confidently compared to this species are known, it is treated as a previously undescribed genus and species.

It would be unwise at this stage to draw any firm conclusions about the phylogenetic relations of this taxon. The simple cardinalia and brachial loop structure seen in the transverse serial sections (Fig. 2), is unusual and suggests a late Jurassic or early Cretaceous ancestry. However, the taxon should remain broadly assigned until more material is obtained, allowing further investigation.

OCCURRENCE. All specimens came from the *Loftusia*-rich facies (beds 3–6) Jebel Huwayyah, section 2 (see volume Introduction for locality details). They are Maastrichtian in age.
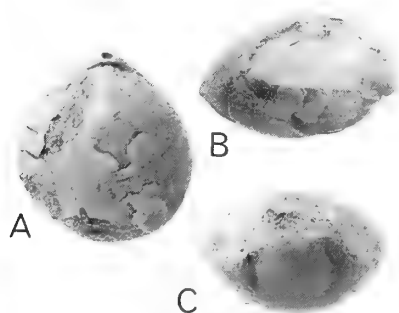
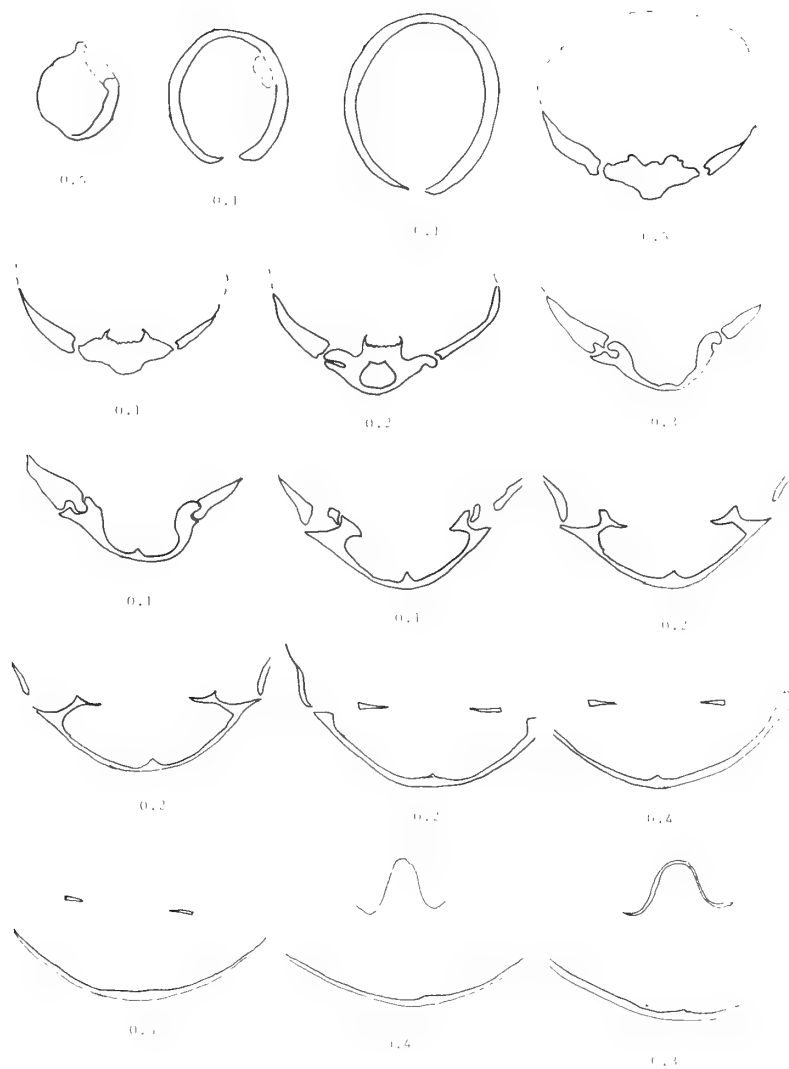**Fig. 2.** Sixteen transverse serial sections through the holotype of *Pseudogibbithyris arabica* gen. et sp. nov. (BMNH BF47) from Jebel Huwayyah, section 2, beds 3–6. Note the bifid cardinal process (sections 5 & 6), the short triangular hinge-plates, and high, arcuate transverse band of the brachial loop. The numerals denote the distance in mm between each section. All × 3.

Late Campanian-Maastrichtian rudists from the United Arab Emirates-Oman border region

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CONTENTS

SYNOPSIS. About 30 species of Upper Campanian and Maastrichtian rudist bivalves from the Qahlah and Simsima Formations of the United Arab Emirates-Oman border region are described. They include *Semailia smithi* gen. et sp. nov. of the Dictyoptychidae, *Glabrobournonia arabica* gen. et sp. nov. of the Radiolitidae (Biradiolitinae), and *Pseudosabinia* gen nov. of the Radiolitidae (Joufiinae). The geological succession at Qarn Mulayh (Mileih), 7 km west of Jebel Buhays, is described.

STRATIGRAPHY AND AGE

In addition to the stratigraphy outlined by Smith, Morris and Gale at the beginning of this volume we include here stratigraphical details of the successions at Qarn Mulayh and Qarn Murrah (the 'red qarns') situated to the west of Jebels Buhays and Faiyah, UAE (Smith *et al.*, this volume, fig. 4). At these localities, limestone platform sedimentation on the serpentinized front of the Semail Ophiolite started earlier than in the jebels to the east, and is equivalent in age to the arenaceous facies of the Qahlah Formation.

A section at Qarn Mulayh is given in Fig. 1. Similar beds also form the majority of the outcrop at Qarn Murrah, to the north. On the basis of the rudists, we suspect that the succession at both qarns is of late Campanian age, and may possibly extend into the earliest Maastrichtian. These limestones correlate laterally with the sandy facies of the Qahlah Formation, with only a few of the species present above in the basal beds of the Simsima Formation.

Table 1 gives a full list of the rudists collected, and their distribution is shown in Fig. 2. The oldest fauna (1 on Fig. 2) occurs at Qarn Mulayh and Qarn Murrah, and also in the lower Qahlah Formation gravels at Jebels Huwayyah and Bu Milh. It is probably Campanian in age (the M1 fauna of Skelton *et al.*, 1990). The middle fauna (2 on Fig. 2) occurs in the upper Qahlah Formation *Loftusia*-Beds at Jebel Huwayyah, and the top Qahlah Formation gravels (with acteonellids) at Jebel Bu Milh. It is Campanian/early Maastrichtian in age (the intermediate M1/M2 fauna of Skelton *et*

al., 1990). The upper fauna (3 on Fig. 3) occurs in the main part of the Simsima Formation, at Jebels Faiyah, Buhays, Rawdah and Huwayyah. It is Maastrichtian in age.

The level 1 fauna compares closely with the so-called *Pironaea-Pseudopolyconites* Senonian fauna of Sladić-Trifunović (1989), for which the type area is the 'Vrbovać Beds' of eastern Serbia. Diagnostic novel taxa (not present in the older Gosau Beds) are: *Pironaea, Yvaniella, *Pseudopolyconites, Joufia, Neoradiolites, Branislavia (? = *Colveraia), Sabinia [= *Pseudosabinia here), and *Mitrocaprina* (asterisks denote those also in the UAR/Oman fauna). In addition, the following were noted by Sladić-Trifunović: *Vaccinites loftusi, V. ultimus, V. orientalis, V. bacevicensis, Hippurites colliciatus, ?*H. lapeirousei, *Hippuritella cornucopiae.* Moreover, Sladić-Trifunović (1989: 149) observed: 'The species *Vaccinites oppeli* Douvillé, also found in the Vrbovać Reef (Bačevića), is certainly of a special biostratigraphic importance, since it was previously believed to exist only in Early Senonian'.

Sladić-Trifunović (1989: 153), following the earlier works of Milovanović and Grubić, regarded the assemblage as Upper Campanian/Maastrichtian, mainly based on the supposed evolution of *Pironaea*. She did, however, acknowledge the arguments of others (for an earlier-extending range), based on orbitoids, and agreed that the fauna was probably absent from the Upper Maastrichtian. Pejović & Radoičić (1987) for example, had revised the age of the 'Brač Marbles' (with *Pironaea* etc) to the Lower-Middle Campanian. Sladić-Trifunović (1989: 154) responded: 'If the 'Brač Marbles', which include *P. milovanovici* [Kühn's species, regarded as

Table 1 Systematic list of the rudists found in the Qahlah and Simsima Formations.

Family CAPROTINIDAE Gray, 1848
    Genus *GYROPLEURA* Douvillé, 1887
      Gyropleura sp.

Family PLAGIOPTYCHIDAE MacGillavry, 1937
    Genus *PLAGIOPTYCHUS* Matheron, 1843
      Plagioptychus cf. *toucasianus* Matheron, 1843

Family DICTYOPTYCHIDAE Skelton *in* Skelton and Benton, 1993
    Genus *DICTYOPTYCHUS* Douvillé, 1905
      Dictyoptychus morgani (Douvillé, 1904)
    Genus *EODICTYOPTYCHUS* Skelton & El-Asa'ad, 1992
      Eodictyoptychus aff. *arumaensis* Skelton & El-Asa'ad, 1992
    Genus *SEMAILIA* Morris & Skelton, gen. nov.
      Semailia smithi Morris & Skelton sp. nov.
      Semailia sp.

Family HIPPURITIDAE Gray, 1848
  Subfamily TORREITINAE Grubić, 1979
    Genus *Torreites* Palmer, 1933
      Torreites sanchezi (Douvillé, 1927) *milovanovici* Grubić, 1980
  Subfamily HIPPURITINAE Gray, 1848
    Genus *VACCINITES* Fischer, 1887
      Vaccinites loftusi (Woodward, 1855)
      Vaccinites vesiculosus (Woodward, 1855)
      Vaccinites oppeli (Douvillé, 1892)
    Genus *HIPPURITES* Lamarck, 1801
      Hippurites aff. *lapeirousei* Goldfuss, 1841
      Hippurites cornucopiae Defrance, 1821
      Hippurites aff. *cornucopiae* Defrance, 1821
    Genus *PIRONAEA* Meneghini *in* Pirona, 1868
      Pironaea cf. *polystyla* Pirona, 1868

Family RADIOLITIDAE d'Orbigny, 1847
  Subfamily RADIOLITINAE d'Orbigny, 1847
    Genus *Praeradiolites* Douvillé, 1902
      Praeradiolites cf. *subtoucasi* Toucas, 1907
    Genus *Radiolites* Lamarck, 1801
      ?*Radiolites* sp.
  Subfamily PSEUDOPOLYCONITINAE Sladić-Trifunović, 1983
    Genus *Pseudopolyconites* Milovanović, 1937
      Pseudopolyconites aff. *parvus* Milovanović, 1935
  Subfamily BIRADIOLITINAE Douvillé, 1902
    Genus *Biradiolites* d'Orbigny, 1850
      Biradiolites aff. *baylei* Toucas, 1909
      ?*Biradiolites* aff. *baylei* Toucas, 1909
    Genus *Glabrobournonia* Morris & Skelton gen. nov.
      Glabrobournonia arabica Morris & Skelton sp. nov.
  Sub-family SAUVAGESIINAE Douvillé, 1908
    Genus *Durania* Douvillé, 1908
      Durania cf. *gaensis* (Dacqué, 1903)
      Durania cf. *apula* (Parona, 1900)
      Durania form A
      Durania form B
      Durania spp.
  Subfamily LAPEIROUSIINAE Kühn, 1932
    Genus *Lapeirousia* Bayle, 1878
      Lapeirousia sp.
    Genus *Osculigera* Kühn, 1932
      Osculigera cf. *vautrinioides* Vogel, 1970
  Subfamily JOUFIINAE Karacabey-Öztemür 1981
    Genus *Colveraia* Klinghardt, 1921
      Colveraia aff. *variabilis* Klinghardt, 1921
    Genus *Pseudosabinia* Morris & Skelton gen. nov.
      Pseudosabinia aff. *klinghardti* (Boehm, 1927)

'advanced'], were accepted as being of the Upper Campanian age, there would be no sense in talking about the evolution of the genus *Pironaea*'. The *Pironaea* story has, indeed, been shown to be incorrect by J. M. Pons & E. Vicens (unpublished), who suggested that the different forms reflect ontogeny, rather than phylogeny, while Swinburne (1990: 27) dated the Brač Marbles (= Pučisča Formation) as early-middle Campanian, based on Sr isotope correlations, in agreement with Pejović & Radoičić. Moreover, by the same means, she and others (Swinburne *et al.*, 1992) re-assigned some *Pironaea* beds in Bulgaria, which had previously been placed at various levels in the Maastrichtian, to the Campanian and lowest Maastrichtian. Thus the '*Pironaea-Pseudopolyconites* Senonian' fauna seems to have ranged from the early Campanian to the earliest Maastrichtian. Additionally, Philip & Platel (1987) assigned their *Torreites* beds in Dhofar to the Campanian, based on orbitoids, while in the Caribbean the range of *Torreites sanchezi* (in our level 1 fauna) is also restricted to the Campanian (Rojas, Iturralde-Vinent, & Skelton, *in press*).

In summary, a Campanian age for the level 1 fauna seems the most plausible (though on the rudist evidence alone, we still cannot yet exclude the earliest Maastrichtian). On the other hand, the level 3 fauna presents a marked contrast, having only *V. oppeli*, *H. cornucopiae*, *Colveraia* and *Pseudosabinia* in common with the classic *Pironaea-Pseudopolyconites* Senonian fauna. *H. cornucopiae*, though, is also well known from the Maastrichtian of Sicily and elsewhere. As noted in Skelton *et al.* (1990: 545), this younger fauna is also characterized by some distinctive Arabian/Iranian endemics (e.g. *Dictyoptychus*). The Level 3 fauna is independently dated by ammonites (Kennedy, this volume) as late Early to early Late Maastrichtian.

SYSTEMATIC PALAEONTOLOGY

Most of the described and figured rudists are in the collections of The Natural History Museum, and are cited with the prefix BM; many of them have the additional prefix LL, and unless otherwise stated the specimens are in the Morris, Gale & Smith Collection; most of the other material is in the Skelton collection, collected by Skelton and Nolan (Skelton *et al*, 1990). The morphotype nomenclature used, eg. 'elevator', 'clinger', 'recumbent', is according to the scheme of Gili & Skelton (1994), summarised by Skelton (1991) and Ross & Skelton (1993).

Family **CAPROTINIDAE** Gray, 1848.
(*emend.* Skelton, 1978; =Monopleuridae Munier-Chalmas, 1873)
Genus ***GYROPLEURA*** Douvillé, 1887

TYPE SPECIES. *Requienia cenomanensis* d'Orbigny, 1850.

REMARKS. There are no accessory cavities.

***Gyropleura* sp.**   Pl. 1, fig. 2

MATERIAL. Four small specimens from top bed 4 or basal bed 5, Simsima Formation Jebel Rawdah, section 1, ammonite and inoceramid horizon; two are attached to the upper valve of an '*Umbonium*', BM LL41767–69.
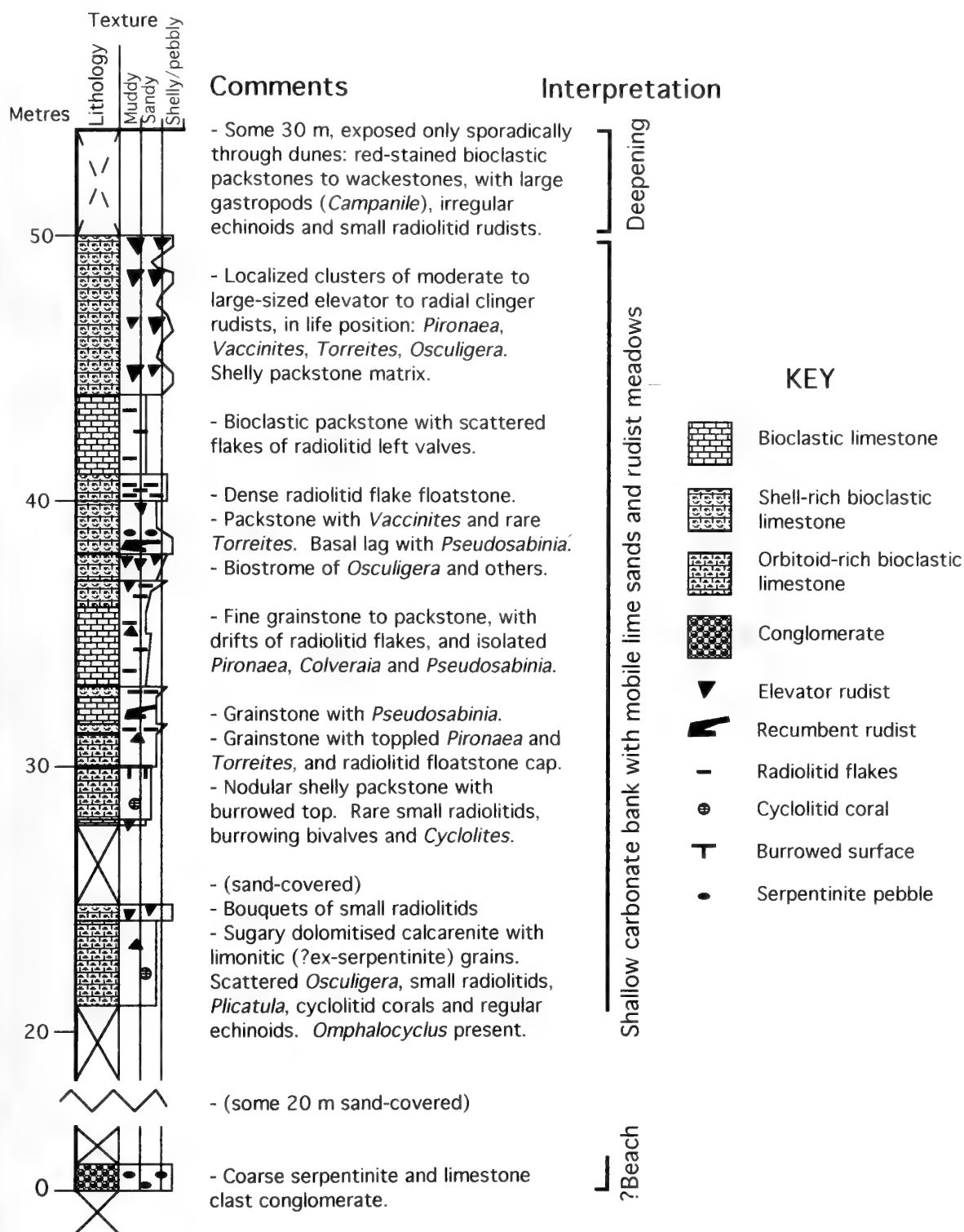
Texture

Lithology | Muddy | Sandy | Shelly/pebbly

Metres

Comments

Interpretation

- Some 30 m, exposed only sporadically through dunes: red-stained bioclastic packstones to wackestones, with large gastropods (*Campanile*), irregular echinoids and small radiolitid rudists.

- Localized clusters of moderate to large-sized elevator to radial clinger rudists, in life position: *Pironaea*, *Vaccinites*, *Torreites*, *Osculigera*. Shelly packstone matrix.

- Bioclastic packstone with scattered flakes of radiolitid left valves.

- Dense radiolitid flake floatstone.
- Packstone with *Vaccinites* and rare *Torreites*. Basal lag with *Pseudosabinia*.
- Biostrome of *Osculigera* and others.

- Fine grainstone to packstone, with drifts of radiolitid flakes, and isolated *Pironaea*, *Colveraia* and *Pseudosabinia*.

- Grainstone with *Pseudosabinia*.
- Grainstone with toppled *Pironaea* and *Torreites*, and radiolitid floatstone cap.
- Nodular shelly packstone with burrowed top. Rare small radiolitids, burrowing bivalves and *Cyclolites*.

- (sand-covered)
- Bouquets of small radiolitids
- Sugary dolomitised calcarenite with limonitic (?ex-serpentinite) grains. Scattered *Osculigera*, small radiolitids, *Plicatula*, cyclolitid corals and regular echinoids. *Omphalocyclus* present.

- (some 20 m sand-covered)

- Coarse serpentinite and limestone clast conglomerate.

Deepening

Shallow carbonate bank with mobile lime sands and rudist meadows

?Beach

KEY

▨ Bioclastic limestone

▨ Shell-rich bioclastic limestone

▨ Orbitoid-rich bioclastic limestone

▨ Conglomerate

▼ Elevator rudist

◢ Recumbent rudist

— Radiolitid flakes

⊕ Cyclolitid coral

⊤ Burrowed surface

● Serpentinite pebble

Fig. 1 Measured section at Qarn Mulayh (Mileih), 7 km west of Jebel Buhays; section logged at the north end of the western flank by P W Skelton.

Ut	Ps	Bi	Bo	Du	La	Os	Pk	Pr	Co	Eo	Se	Di	Pl	Pi	Vl	Vv	Vo	Hc	H	T
3		•	•	•	•	?	?		•		•	•	•				•			
2		•	•	•									•	•			•			
1	•		•		?		•	•	•	•	•					•	•	•			•

Fig. 2 Stratigraphical distribution of the rudists. Ut = stratigraphical units: 1 = lower part of the Qahlah Formation, 2 = upper part of the Qahlah Formation (the gravels and the *Loftusia*-Beds), 3 = Simsima Formation. Ps = *Pseudopolyconites*, Bi = *Biradiolites*, Bo = *Glabrobournonia*, Du = *Durania*, La = *Lapeirousia*, Os = *Osculigera*, Pk = *Pseudosabinia* aff. *klinghardti*, Pr = *P. 'rtanjica'*, Co = *Colveraia*, Eo = *Eodictyoptychus*, Se = *Semailia*, Di = *Dictyoptychus*, Pl = *Plagioptychus*, Pi = *Pironaea*, Vl = *Vaccinites loftusi*, Vv = *Vaccinites vesiculosus*, Vo = *Vaccinites oppeli*, Hc = *Hippurites cornucopiae*, H = *Hippurites* aff. *lapeirousei*, T = *Torreites*.

DESCRIPTION. All four specimens have the valves conjoined, with the upper left valve slightly exogyriform and the lower valve rather longer but with considerable variation in size of attachment surface; line of commissure slightly sinuous. Outer shell surface of both valves with fine, evenly and closely spaced, radiating striiform ribs. Shell margins crenulate. Adductor attachments visible in the left valve of specimen LL41767 on concave surfaces of the hinge plate, a little below the plane of commissure. *Gyropleura* is a clinger.

Family **PLAGIOPTYCHIDAE** MacGillavry, 1937: 105, 152
(*ex.* Plagioptychinae MacGillavry, 1937 (plagioptychinés Douvillé, 1888: 729))
Genus ***PLAGIOPTYCHUS*** Matheron, 1843.

TYPE SPECIES. *Plagioptychus paradoxus* Matheron, 1843, subsequently designated by Kutassy (1934: 172).

REMARKS. Species of *Plagioptychus* are clingers to low elevators.

Plagioptychus* cf. *toucasianus Matheron, 1843 Pl. 1, fig. 1

cf. 1843   *Plagioptychus toucasianus* Matheron, 117.

MATERIAL. Two small specimens from near the base of the Simsima Formation at Jebel Faiyah, BM LL41765 (centre), LL41766 (from section 2), Skelton Collection.

DESCRIPTION. Inequivalve, right valve smaller than free left valve, exogyriform with sinuous commissural margin with large attachment area, surface slightly rugose with prominent commarginal growth lines. The rather short exterior dorsal surface has a sub-vertical ligament groove and the shell surface bulges to the posterior of this line. Outer calcitic shell layer thin to medium, with thin inner layer without pallial canals. Prominent tooth and attached myophore projects into upper valve.

Free left, upper valve globose, regularly coiled, gryphaeate with smooth surface; outer calcitic shell layer thin, inner layer recrystallized to calcite but medium to thick, with radially elongated narrow canals that do not pass into polygonal structure and in that way differ from *Mitrocaprina* or the upper valve of *Coralliochama*. The narrow canals also do not bulge internally as is common in some forms of the genus. Anterior myophore robust and nearly level with the commissure. An oblique septum runs from the anterior tooth to the ventral margin. The cavity posterior to this septum houses the large central tooth and conjoined posterior myophore in a dorsal position.

Family **DICTYOPTYCHIDAE** Skelton *in* Skelton & Benton, 1993
(*ex.* Trechmannellidae Cox, 1933: 65)

DIAGNOSIS. Inequivalved rudists, attached by right valve. Valves uncoiled and ligament absent. Outer (calcitic) shell layer compact. Inner (originally aragonitic) shell canaliculate throughout, in both valves. Two projecting teeth in left valve, straddling ridge-like central tooth in right valve. Posterior tooth dorso-ventrally flattened, flanking body-cavity, and separated from the dorsal margin by a small accessory cavity, which may be a relic of the ligamentary cavity. Anterior myophoral platforms extended both dorsally on hinge plate, around anterior tooth, and ventrally from hinge plate. Posterior myophore of left valve projecting, with adductor scar facing outwards, into recess, or socket, in posterior wall of right valve, and directly flanking body-cavity.

REMARKS. The distinctive features of this family were discussed, in relation to *Eodictyoptychus,* by Skelton and El-Asa'ad (1992). The dictyoptychid myocardinal apparatus differs from that seen in the Caprinidae (s.s.), the Plagioptychidae, and *Sabinia* (s.s.) in all of which the posterior tooth and posterior myophore (with *inward*-facing muscle scar) of the left valve are separated from the body-cavity by the combined central tooth socket and an accessory cavity, extending ventrally from it, which receives the salient myophore of the right valve. The latter cavity is itself demarcated by a prominent lamina running from the anterior tooth to the postero-ventral margin of the valve. No equivalents of this lamina, and the associated accessory cavity, are present in the left valve of dictyoptychids.

Pseudosabinia (Radiolitidae) differs in its possession of a

PLATE 1
Fig. 1 *Plagioptychus* cf. *toucasianus* Matheron, from Jebel Faiyah, lower part of Simsima Formation. **1a**, anterior view, **1b**, section through left valve approximately 5 mm from the commissure, BM LL41766, × 1, Skelton Collection **1c**, dorsal view, BM LL41765, × 1.
Fig. 2 *Gyropleura* sp., from Jebel Rawdah, section 1, loose from top of bed 2 or bed 3 of Simsima Formation; **1a**, posterior view, **1b**, dorsal view, **1c**, view looking down on left valve, BM LL41768, × 2.
Fig. 3 *Dictyoptychus morgani* (Douvillé), from Jebel Buhays, section 1, bed 11 of Simsima Formation, side view, BM LL41680, × 0·5.
Fig. 4 *Eodictyoptychus arumaensis* Skelton & Al-Asa'ad, from Jebel bu Milh, section 1, top of Qahlah or basal Simsima Formation; **4a**, top view, **4b**, internal view, **4c**, dorsal view, BM LL41927, left valve, × 1·5.

ligamentary invagination, and the presence of celluloprismatic structure in the outer shell layer of the right valve. Despite the similarity to the Antillocaprinidae MacGillavry, 1937, in their lack of a ligament, and the presence of the small dorsal accessory cavity, which may be a relic of it, the dictyoptychids differ from *Antillocaprina* (at least) in having the posterior myophore of the left valve projecting, rather than parallel with the plane of commissure. Moreover, the outer shell layer of antillocaprinids is invariably very thin, whilst that of dictyoptychids is usually relatively thick in the right valve.

Genus *DICTYOPTYCHUS* Douvillé, 1905.
(*nom. nov.* for *Polyptychus* Douvillé 1904, *non* Huebner, 1816)

TYPE SPECIES. *Polyptychus morgani* Douvillé, 1904, by monotypy.

SYNONYM. *Trechmannella* Cox, 1933 (obj.).

REMARKS. Attached right valve with large polygonal canalicular structure. Outer layer of right valve thicker than that of left valve, with exposed growth margin; sharply peaked ridges on right valve growth margin in some specimens. We agree with Pons *et al.*, 1992, who regard all described species as probably synonymous.

Dictyoptychus morgani (Douvillé, 1904)   Pl. 1, fig. 3

1904   *Polyptychus morgani* Douvillé: 248–51, pl. 33 bis.
1905   *Dictyoptychus morgani* (Douvillé); Douvillé: 198.

MATERIAL. Jebel Faiyah, section 1, bed 3, BM LL41670–71; section 2, LL41659; Jebel Faiyah, centre, LL41683–84. Jebel Aqabah, Simsima Formation, loose, BM LL41676. Jebel Thanais, Simsima Formation, loose in scree, BM LL41668–69. Jebel Buhays, section 1, bed 11, LL41677, 41680; section 1b, LL41674; section 1a, Simsima Formation, BM LL41675. Jebel Rawdah, section 1, bed 3, BM LL41657–58, 41679, 41681; section 2, bed 19, LL41673; section 2, loose on scree, LL41667; section 4, bed 1, LL41672; Jebel Rawdah, north, LL41690. Jebel Bu Mihl, section 1, bed 3, BM LL41660–66. Jebel Huwayyah, section 2, beds 3–5, BM LL41678; Jebel Huwayyah, LL41685–89. Jebel Sa'ah, basal Simsima Formation, BM LL41682.

REMARKS. Occurs widely in the lower half of the Simsima Formation, sometimes in great numbers. *Dictyoptychus* is a multigeniculate elevator (see Ross & Skelton, 1993: fig. 5.2).

Genus *EODICTYOPTYCHUS* Skelton & El-Asa'ad, 1992

TYPE SPECIES. *Eodictyoptychus arumaensis* Skelton & El-Asa'ad, 1992, by original designation.

Eodictyoptychus aff. *arumaensis* Skelton & El-Asa'ad, 1992.   Pl. 1, fig. 4; Pl. 2, fig. 2

v   aff. 1992   *Eodictyoptychus arumaensis* Skelton & El-Asa'ad: 108–13, pl. 1, figs 1–6.

MATERIAL. Jebel Bu Milh, section 1, Qahlah/Simsima Formation Boundary, BM LL41927–8; section 2, LL41929; all are left valves. A possible fragment of a right valve from Qarn Murrah, BM LL41977, Skelton Collection.

DESCRIPTION. Moderately inaequivalved, free left valve with thin outer calcitic shell layer, inner aragonitic layer recrystallised but formed of varyingly sized canals of polygonal section, even within the teeth and the massive myophores. Two subequal, projecting teeth in free valve, the anterior one below the umbo, the smaller, posterior one ventral to this, the two separated by a socket whose centre lies above and towards the umbo from the posterior tooth. The teeth lie on the body-cavity side of a massive plate which includes the attachment surfaces of the myophores, and takes up more than half of the area within the valve when looking down on the commissural plane.

We have not been able to detect the accessory cavity dorsal to the posterior tooth, but this may be due to the difficulty of its preparation. The projecting posterior myophore is separated from the body-cavity by a narrow ledge which is not present in the type material from Khashm Buwaibiyat, approximately 50 km north of Riyadh.

REMARKS. *Eodictyoptychus* varies from a lateral clinger to a recumbent.

Genus *SEMAILIA* Morris & Skelton, gen. nov.

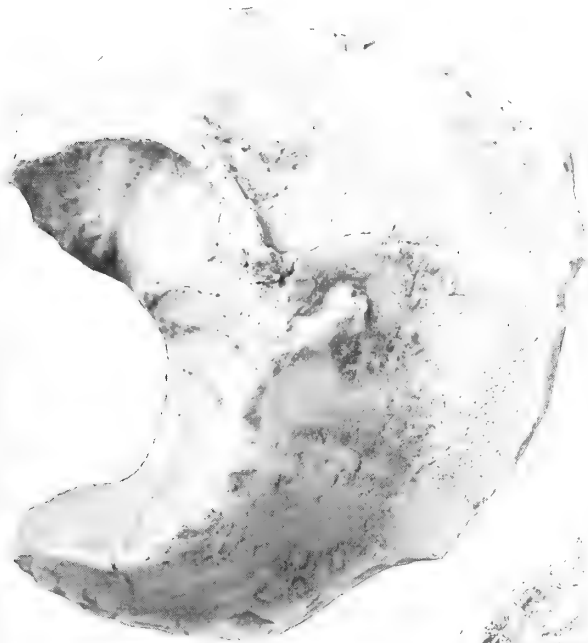TYPE SPECIES. *Semailia smithi* Morris & Skelton gen. et sp. nov.

DIAGNOSIS. Bicornate and multicarinate, subequivalve with a thin outer shell layer in each valve. Inner shell canaliculate in both valves. Myocardinal arrangement typical of dictyoptychids with two teeth in the left valve, the posterior tooth dorso-ventrally flattened and flanking the body-cavity without an intervening accessory cavity. No ligament present. The posterior myophore of the left valve projecting into a socket in the right valve, again flanking the body-cavity without an intervening accessory cavity.

REMARKS. The absence of a posterior accessory cavity in the left valve excludes this taxon from the Caprinidae, Plagioptychidae and *Sabinia* s.s., and the outward facing, ie monopleuriform, myophores, are typical of the dichtyoptychid plan. Unlike other members of the Dictyoptychidae this genus does not show the differentially greater thickening of the outer calcitic layer of the right valve.

PLATE 2

Fig. 1   *Semailia smithi* Morris & Skelton, gen. & sp. nov. Jebel Huwayyah, section 2, *Loftusia*-Beds; **1a**, anterior view, **1b**, posterior view, **1c**, view of right valve, **1d**, dorsal view; holotype. BM LL41931, × 1.

Fig. 2   *Eodictyoptychus* aff. *arumaensis* Skelton & Al-Asa'ad, Jebel bu Milh, section 1, top of Qahlah or base of Simsima Formation; internal view of left valve, BM LL41928, × 1.
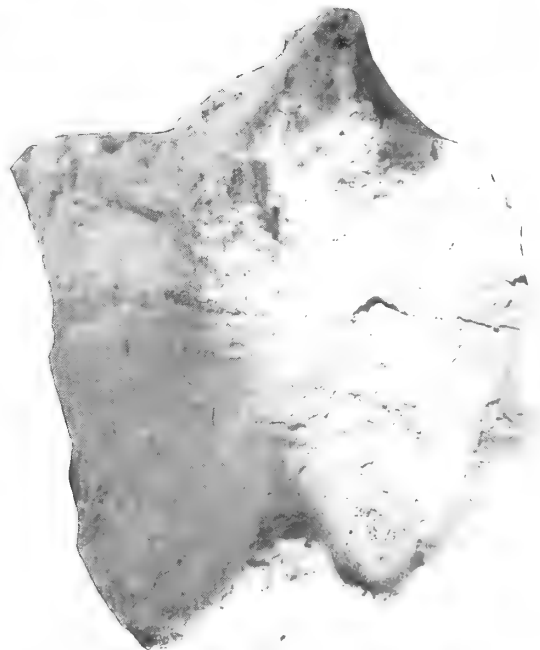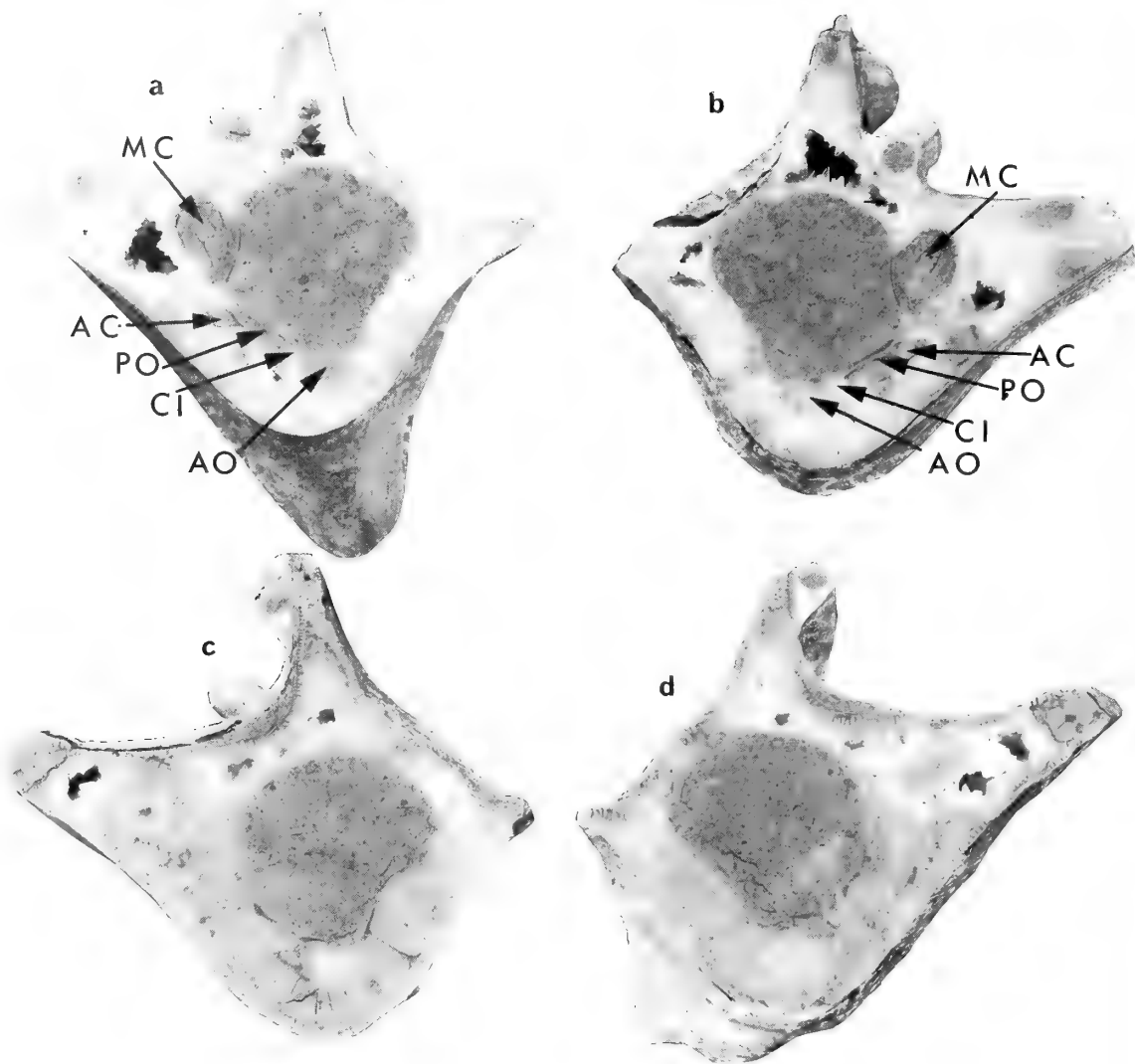
1a

1c

2

1b

1d

Fig. 3 *Semailia smithi* Morris & Skelton sp. nov. Four sections through the holotype approximately 10 mm either side of the commissure, BM LL41931; **a, b**, right valve, MC – accessory cavity for posterior myophore of left valve, PO – posterior tooth socket, AC – accessory cavity dorsal to tooth socket, CI – central tooth, AO – anterior tooth socket; **c, d**, left valve, with fine outer and large irregularly polygonal inner canals; × 1.

PLATE 3

Fig. 1 *Semailia* sp., Jebel bu Milh,section 2, base of Simsima Formation; **1a**, ventral view of broken right valve, **1b**, dorsal view of right valve; BM LL41932 × 0·75.

Fig. 2 *Torreites sanchezi milovanovici* Grubić; Haushi-Huqf Massif, Eastern Oman, BM LL41975, Samir Hanna Collection; **2a**, view looking down onto commissural plane with broken left valve partly preserved in situ, × 1; **2b**, dorsal view showing intucking of pillar L, **2c**, posterior view showing infolds of pillars, **2d**, ventral view; 2b–d, × 0·5.

Fig. 3 *Vaccinites* aff. *oppeli* (Douvillé), Jebel bu Milh, section 2, Simsima Formation, bed 10, BM LL41730, marginal surface of outer shell layer of right valve, × 1.

Semailia smithi Morris & Skelton sp. nov.   Pl. 2, fig. 1, Fig. 3

MATERIAL. A single specimen, the holotype, BM LL41931, from Jebel Huwayyah, section 2, *Loftusia*-Beds.

DIAGNOSIS. Typical of the genus but with three strong carinae or flaring radial costae on each valve.

DESCRIPTION. Both valves are preserved, closed, although the body-cavity is matrix-filled and includes larger foraminifera. The specimen has two serpulids attached, one to each valve and aligned radially with respect to the umbones, with their apertures close to the valve commissure, amid the plicae of the ventral margins.

The shell is curvingly biconical, with the two valves separately following almost a semicircular direction of growth, in

1a

1b

2a

2b

2c

2d

3
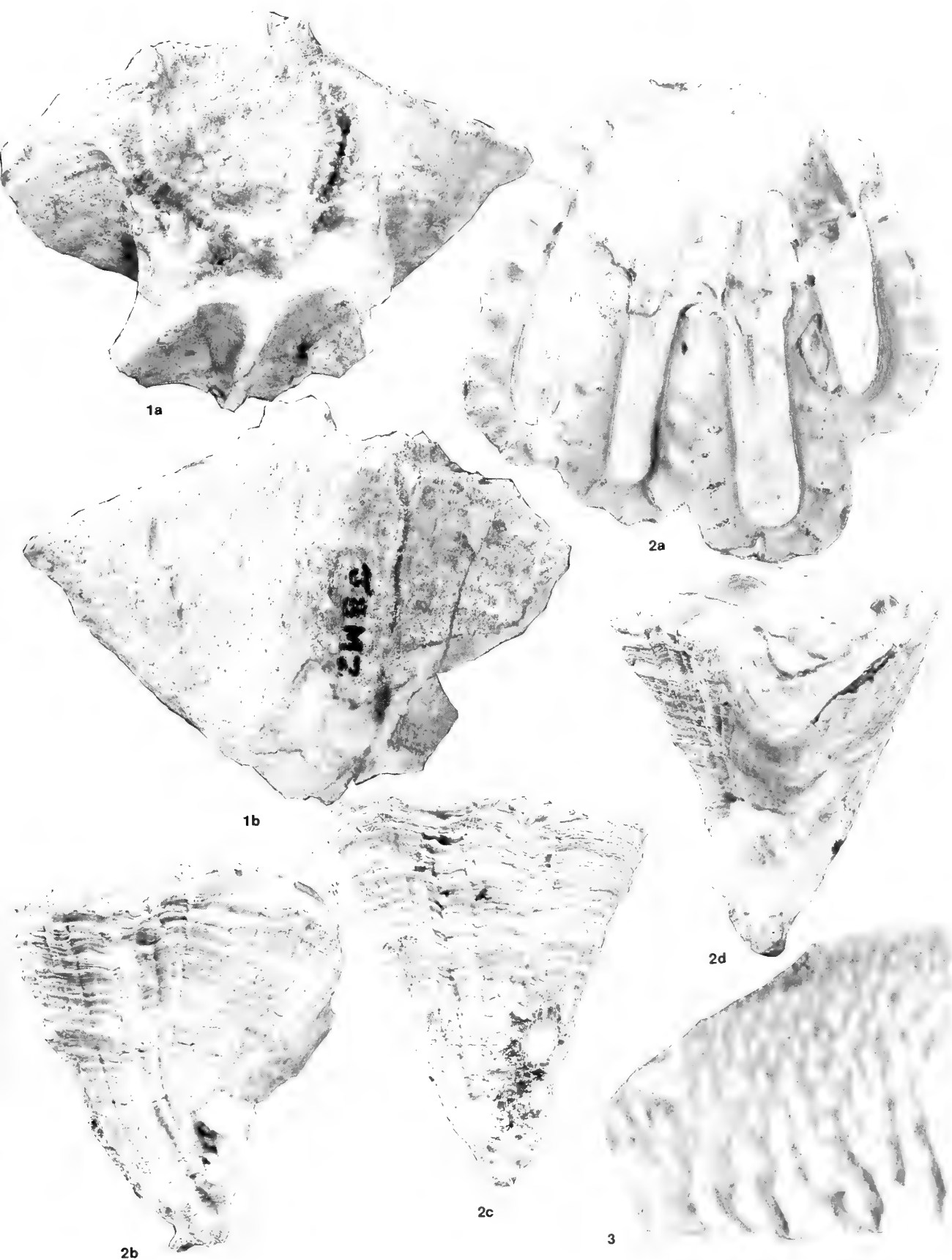
a single plane, so that the umbones or apices are beginning to approach each other; sub-equivalve with the right valve slightly 'longer' than the left. Three prominent carinae or flaring radial costae, skewed to the posterior, two at approximately 180°, set anteriorly and posteriorly on both valves and the third normal to these on the ventral margin. Dorsal margin rounded. Shell surface otherwise relatively smooth on both valves.

No ligament present. Very thin outer calcitic shell layer in both valves. Canals are present in the thick inner shell layer of both valves, round and capillary-like around the margins, becoming larger inside, irregularly rounded polygonal in section, especially in the left valve.

Two teeth in the left valve are typical of the family, the anterior one is rounded and knob-like, the posterior one is dorso-ventrally flattened. One central tooth in the right valve. The posterior myophore of the left valve projects into an accessory cavity (socket) in the right valve. The anterior myophore of the left valve is a broad shelf and has large canals. There is an accessory cavity in the right valve which lies dorsally to the flattened posterior tooth socket.

COMMENTS. The crescentic form of the shell suggests a recumbent life position, possibly reclining on the dorsal flank. It was found in a matrix of marly limestones with large specimens of *Loftusia* with a similar matrix filling the body-chamber, forming a loftusid packstone.

COMPARISON WITH OTHER TAXA. There is a great similarity in the myocardinal arrangement with that of other dictyoptyichids, but *Semailia* differs in having a much thinner outer shell layer in both valves and having strong shell carinae.

Semailia sp.   Pl. 3, fig. 1

MATERIAL. A single specimen from Jebel Bu Milh, section 2, basal Simsima Formation, BM LL41932.

DESCRIPTION. The specimen is a large right valve, its anterior and posterior part nearly symmetrical about a dorso-ventral plane. Multicarinate but otherwise smooth. Two wide anterior and posterior carinae form a wide kite-shape in dorsal view. Dorsal surface flattish near the commissure, but umbones incurved and separating two gently concave anterior and posterior areas with a low mid-dorsal carina that is prominent at the umbo, but faces towards the mid-dorsal margin. Ventral part of shell has three sub-equal strong carinae, which are equidistant from the dorsal margin and inclined towards the anterior.

Outer shell layer thin and now formed of structureless recrystallized blocky calcite. Thick canaliculate inner shell layer with capillary-like polygonal canals throughout, including the teeth, fine at the margins becoming larger inwards, now also recrystallized to calcite.

Right valve has part of projecting stout central tooth preserved behind base of the socket for the anterior tooth of the left valve and in front of the socket of the posterior tooth of the left valve, containing a fragment of that dorso-ventrally flattened tooth.

COMPARISON WITH OTHER SPECIES. *Semailia* sp. differs from *S. smithi* in having two additional ventral carinae. There is not enough material to know if this difference is significant in discriminating separate species.

Family **HIPPURITIDAE** Gray, 1848
Subfamily **TORREITINAE** Grubić, 1980
Genus ***TORREITES*** Palmer, 1933

TYPE SPECIES. *Hippurites (Vaccinites) sanchezi* Douvillé, 1927, by original designation.

DESCRIPTION. Outer shell layer of right valve with tight marginal infoldings, giving rise to radiating crests (Douvillé, 1894) around the shell margin of the right valve, but variable in extent and number. Outer shell layer of left valve thin, postero-dorsally digitiform, smooth except for fine growth lines on the upper surface, but becoming overgrown with epibionts radiating from its low apex. Inner shell layer of both valves partly canaliculate, canals of right valve relatively large, sub-radial and sub-rectangular in section, in the area of the anterior muscle attachment. We have observed a similar reticulate network of vertical ridges separating tabulate canals in the anterior myophoral ledge of *Vaccinites gosaviensis* (BM 33972, a specimen with the original aragonite preserved). The canals of the left valve are narrow and radiate from the apex.

REMARKS. Philip & Platel (1994) pointed to the similarity of *Torreites* with their new genus, *Praetorreites*, from the Lower Campanian, Samhan Formation of south-east Oman. The latter has canaliculate structure of the inner shell layer of the left valve and regular pedunculate radial structures in the outer shell layer of the right valve, which, they claim, are comparable with the radiating marginal crests of *Torreites*. They compare the subfamily, raised to family rank, with both the Plagioptychidae and the Hippuritidae, concluding that the similarity is greater with the Plagioptychidae. If Philip & Platel are correct in their suggestion that the Torreitinae are not hippuritids, then it follows that the three large infolds of the outer shell layer of the right valve are not homologues of the hippuritid pillars. The origin of two of the pillars of *Torreites* is claimed to be from the two small 'pillars' of *Praetorreites* and considered by Philip & Platel to be analogues of pillars 'E' and 'S'. Philip & Platel's plate 8, fig. 1 shows the position of these 'pillars' in relation to the teeth and myophores of the upper valve. If this arrangement is compared with the hinge structures of *Dictyoptychus* (Douvillé, 1904: pl. 33 bis, fig. 4), the alignment of the sockets and teeth is very similar, although they are at a more obtuse angle

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PLATE 4

Fig. 1 *Torreites sanchezi milovanovici* Grubić, Haushi-Huqf Massif, Eastern Oman (also figured Skelton & Wright, 1987: pl. 67, fig. 1), BM LL28004, view looking down onto right valve (note coarse cellular structure of myophore in lower part of figure and tooth sockets to the right of pillar 'L'), × 1.
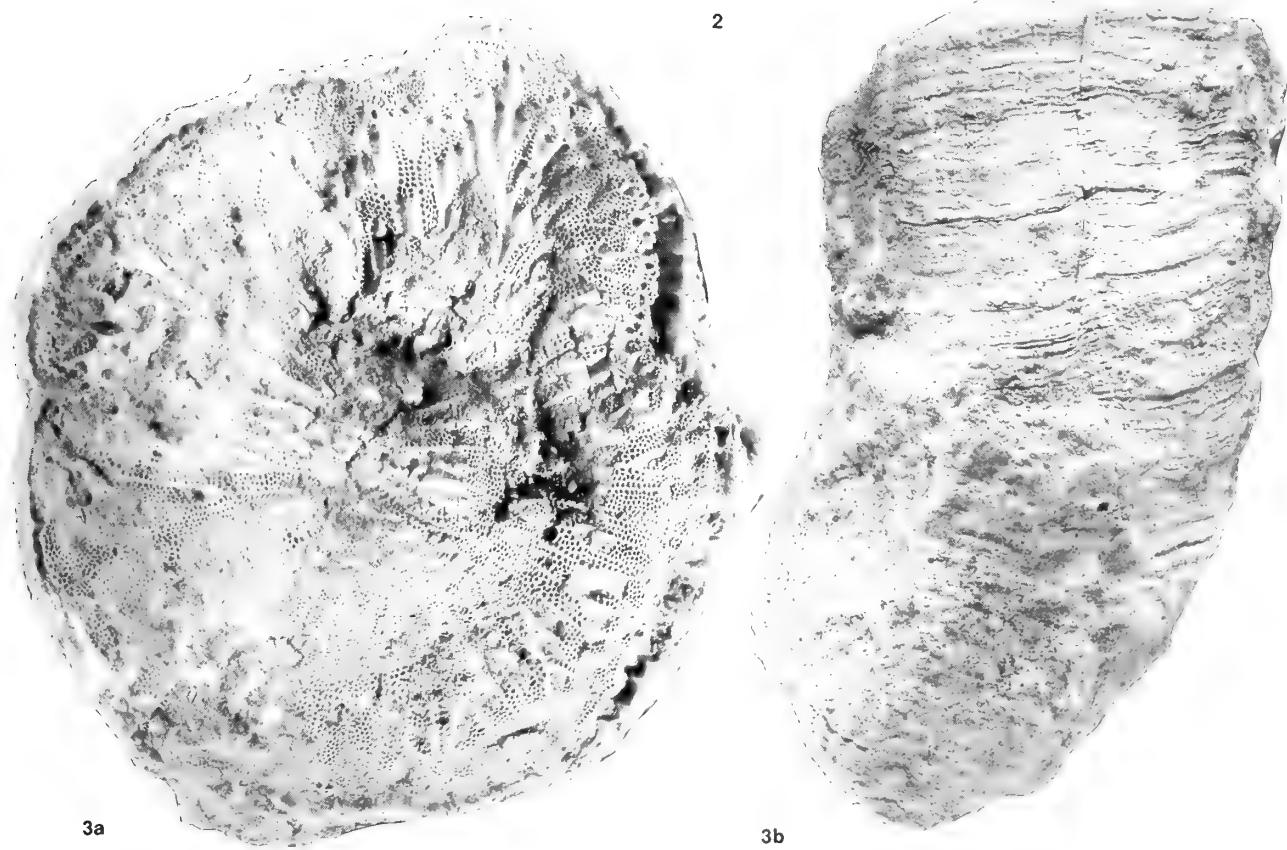
Fig. 2 *Vaccinites* aff. *oppeli* (Douvillé), Jebel bu Milh, section 2, Simsima Formation limestone, BM LL41733, view of naturally broken section of right valve, × 0·4.

Fig. 3 *Vaccinites vesiculosus* (Woodward), Jebel Huwayyah, *Loftusia*-Beds, BM LL41716, Skelton Collection, **3a**, view of partly eroded left valve, **3b**, view of right valve, × 0·5.
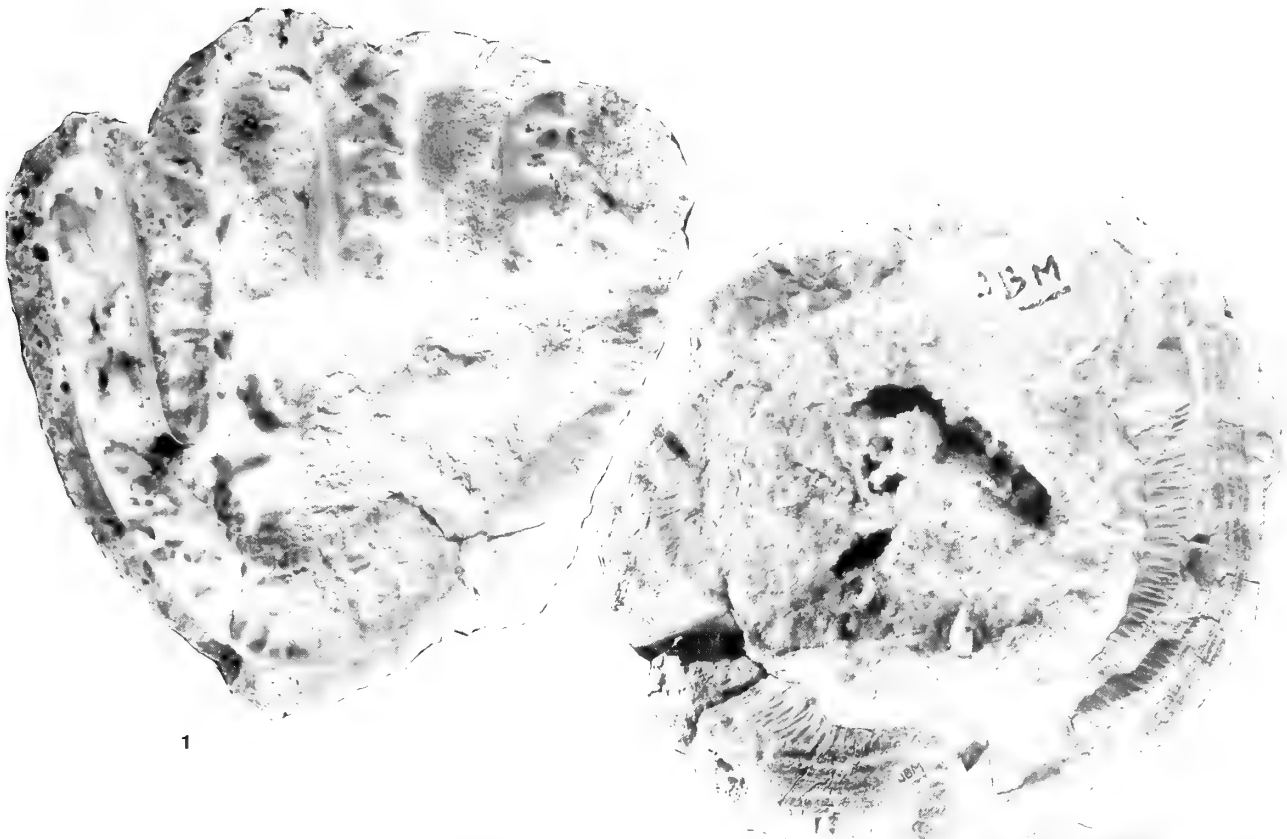
1

2

3a

3b

to the ventral shell margin. This suggests a relationship between *Dictyoptychus* and *Praetorreites*.

It is difficult to relate the anterior infolding of *Torreites* to the position of ligamentary invagination of the plagioptychids, but much easier if *Torreites* is interpreted as a hippuritid. Details of the morphology are illustrated by Skelton & Wright (1987: fig. 2). In Skelton & Wright's interpretation of *Torreites* loss of the hippuritid canal system of the outer shell layer of the left valve is by recurvature of the shell margin to expose the mantle margins. The umbo of the operculiform left valve is close to the ventral margin.

Philip & Platel (1994: fig. 4) claim a diphyletic origin for the 'three-pillared' genus *Torreites* and thus claim to have refuted the palaeobiogeographical interpretation of Skelton & Wright (1987). Their diagram shows *Praetorreites* occurring before *Torreites* and giving rise independently to the Caribbean and Arabian species. However, their date for the small Caribbean species *Torreites tschoppi* on this diagram does not show its full range. There is ample evidence to show that this species is best dated as Santonian in Cuba (Rojas *et al.*, *in press*) and therefore pre-dates Campanian *Praetorreites*. Their analysis leading to the view that the torreitines are not closely related to the hippuritids relies heavily on the interpretation of the ancestral status of *Praetorreites* and the supposed homology of the pedunculate folds, with the marginal radiating crests of *Torreites*, which in the latter are a consequence of tight infoldings of the outer shell surface. A superficially similar structure in section may be seen in the outer shell layer of the lower valve of *Dictyoptychus striatus*, but this is formed as a consequence simply of salient radial ridges on the growth margin of that shell layer, without any infolding of the outer surface. In Philip & Platel's (1994: pl. 7, fig. 3) illustration of *Praetorreites* the similarity, if anything, seems greater with the radial ridges of the dictyophychid, than with the intuckings of *Torreites*. In all particulars *Praetorreites* is similar to *Eodictyoptychus* and appears to have little in common with *Torreites*.

The criticism of Skelton and Wright's (1987) explanation of the distribution of *Torreites* is therefore unconvincing. We maintain the view that the differences between the Caribbean and Arabian *Torreites* do not warrant greater that subspecific separation, and that their similarities do reflect that genetic interchange between the two areas of occurrence did take place.
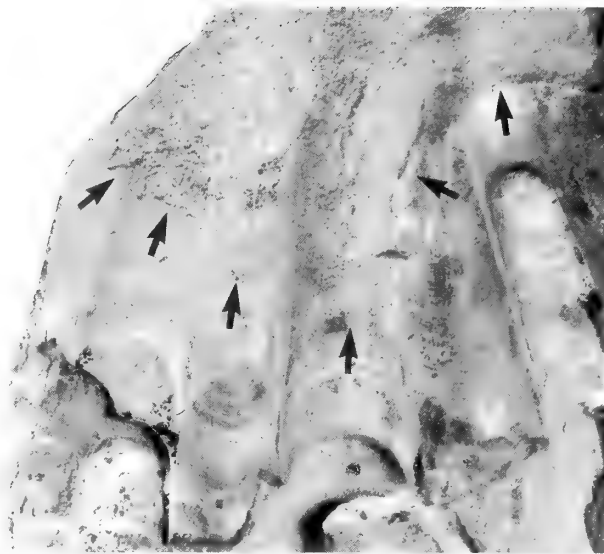

Fig. 4 *Torreites sanchezi milovanovici* Grubić; smooth top surface of left valve with advancing front of epibionts (arrowed), BM LL41975, × 2.
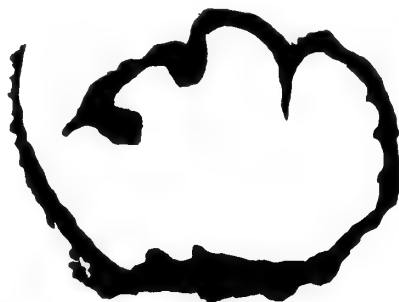

Fig. 5 Camera lucida drawing of *Vaccinites loftusi* (Woodward); from Qarn Murrah, BM LL41933, Skelton Collection, × 1.

Torreites sanchezi (Douvillé, 1927), subsp. *milovanovici* Grubić, 1980

Pl. 3, fig. 2; Pl. 4 fig. 1

1927   *Hippurites (Vaccinites) sanchezi* Douvillé: 54, 55, pl. 4, fig. 1.
1980   *Torreites milovanovici* Grubić: 92, 93, pl. 1, fig. 1, fig. 4.
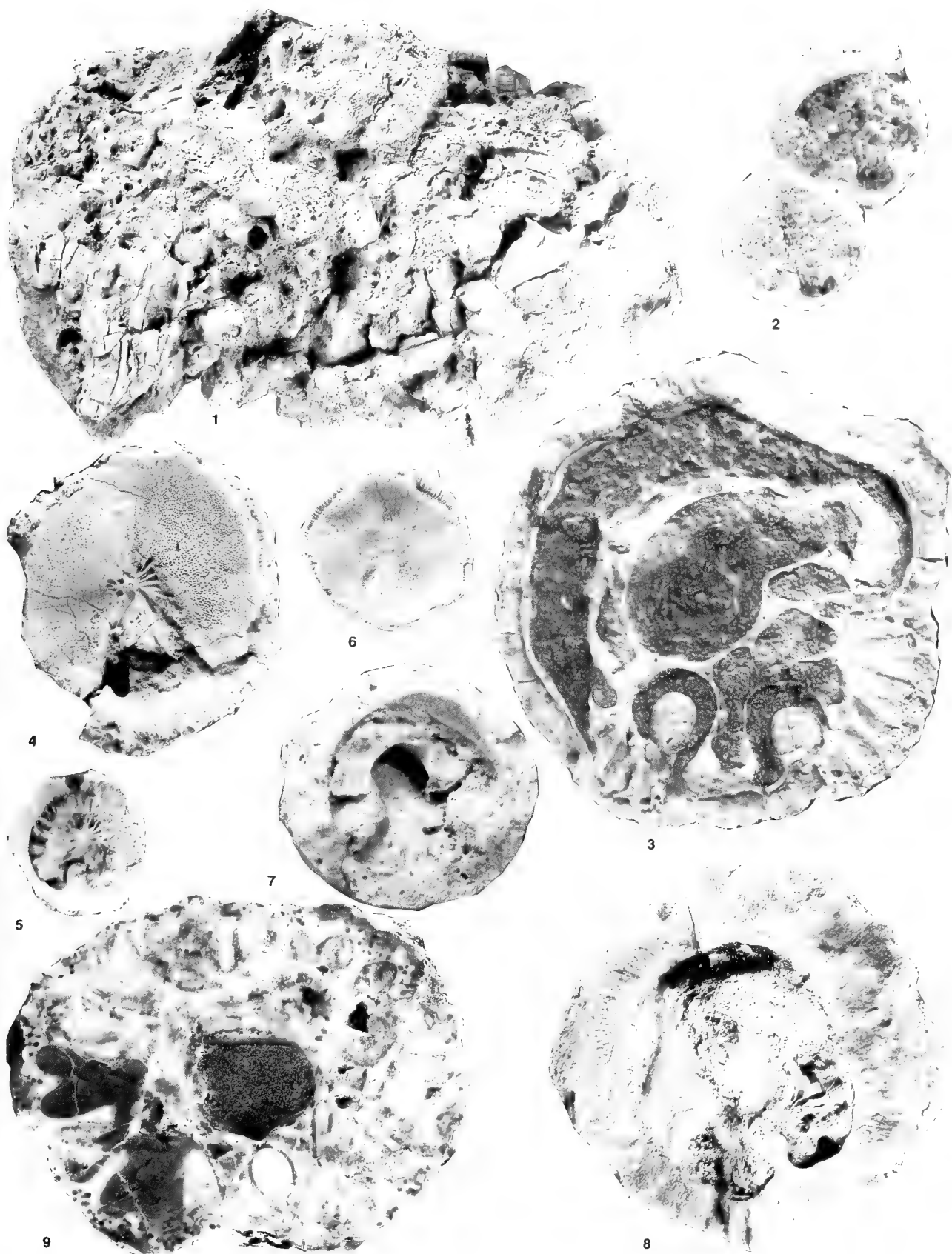

PLATE 5

Figs 1, 2 *Hippurites* aff. *lapeirousei* Goldfuss; **1**, Jebel Faiyah, section 1, Simsima Formation, bed 6, BM LL41754, mass of variously orientated individuals, × 0·5; **2**, Jebel Faiyah, section 1b, Simsima Formation, bed 2, BM LL41755, view looking down onto a pair of right valves, × 2.

Fig. 3 *Vaccinites vesiculosus* (Woodward), Jebel Huwayyah, *Loftusia*-Beds, BM LL41973, V. Chalmers Collection, view looking down on eroded left valve exposing pillars of right valve, × 1.

Figs 4–7 *Hippurites cornucopiae* Defrance; **4–6**, Jebel Faiyah, loose from low in the Simsima Formation, Skelton Collection; **4**, BM LL41747, view of left valve (pores appear polygonal and radially vermiculiform where less eroded), × 1; **5**, BM LL41744, eroded left valve showing pores and canals, × 1; **6**, BM LL41745, view of left valve with oscules and pores appearing vermiculiform or polygonal depending on the degree of erosion, × 1; **7**, BM LL41737, Jebel Thanais, natural section through right valve showing slightly pedunculate pillars, × 1.

Fig. 8 *Hippurites* aff. *cornucopiae* Defrance, Jebel Rawdah, southern flank, loose from Simsima Formation, BM LL41753, Skelton Collection, natural section of right valve, × 0·5.

Fig. 9 *Pironaea* cf. *polystyla* Pirona, Qarn Mulayh, BM LL41938, Skelton Collection, section through right valve, × 1.

1994   *Torreites milovanovici* Grubić; Philip & Platel: pl. 8, fig. 4, fig. 4.
(For further synonymy see Skelton & Wright, 1987)

TYPE SPECIMEN. The holotype of the subspecies is BM LL27699, Iraq Petroleum Company Collection (CP 86), on weathered surface of section, 7·7 m from top at Qarn Mulayh.

OTHER MATERIAL. Two specimens from the same horizon on Qarn Murrah, BM LL41761, 62; a well-preserved specimen showing details of the upper valve, from the Haushi-Huqf Massif, eastern Oman, S. Hanna Collection, BM LL41975; the material of Skelton & Wright (1987) from eastern Oman, BM LL28004; one specimen from Jebel Huwayyah, section 1, Qahlah gravels, BM LL42763; Qarn Mulayh, no specimens collected.

COMMENTS. BM LL41975 shows a boundary between shiny outer shell material and encrusted surface on the outer surface of the upper valve which we interpret as representing the limit of encroachment upon the exposed left mantle surface by epibionts. BM LL28004 shows the loose canalicular structure of the anterior muscle attachment area of the right valve together with the tooth sockets.

Subfamily HIPPURITINAE Gray, 1848
Genus *VACCINITES* Fischer, 1887

TYPE SPECIES. *Hippurites cornuvaccinum* Bronn, 1931, by monotypy.

Vaccinites loftusi (Woodward, 1855)   Fig. 5

1855   *Hippurites loftusi* Woodward: 58, pl. 3 figs 2–3.
1897   *Hippurites loftusi* Woodward; Douvillé: 210, pl. 33 (17), figs 1, 1a, 1b.
1904   *Vaccinites loftusi* (Woodward); Toucas: 82, 83, figs 126, 127.

MATERIAL. Three specimens from Qarn Murrah, BM LL41933, LL41969–70; another from Jebel Huwayyah, *Loftusia*-Beds, LL41934; Skelton Collection.

REMARKS. These specimens have the typical coarse external ribs of Woodward's species but are very poorly preserved internally. The pillars of a Qarn Murrah specimen resemble those of Woodward's type but were not enhanced by sectioning. The pores of the upper valve are in the form of coarse polygons and the outer surface of this left valve has radial undulations. Woodward's type material has incipient multiple infoldings of the outer shell layer of the right valve, reminiscent of *Pironaea*.

Vaccinites vesiculosus (Woodward, 1855)   Pl. 4, fig. 3;
                                                                    Pl. 5, fig. 3

1855   *Hippurites vesiculosus* Woodward: 59, pl. 4, fig. 6.
1897   *Hippurites vesiculosus* Woodward; Douvillé: 201, pl. 29 (13), figs 6, 7.
1904   *Vaccinites vesiculosus* (Woodward); Toucas: 110, 111.

MATERIAL. Qarn Murrah, BM LL41691–7, LL41721–26, Skelton Collection; Jebel Huwayyah, section 1, bed 9, BM LL41698–702; section 2, bed 7 (the main coral bed), BM LL41703–4; section 2, beds 2–7, BM LL41705–15 plus another 9 specimens; Jebel Huwayyah, loose, Skelton Collection, BM LL41716–20, V. Chalmers Collection, BM LL41973; three possible specimens from Jebel Thanais, loose in scree below lowest 3m of the Simsima Formation, BM LL41935–37.

REMARKS. The specimens from the *Loftusia*-Beds at Jebel Huwayyah are larger than either those from Qarn Murrah or Woodward's type material. They however have the same type of pillars in the right valve with a long thin arête cardinal and pedunculate pillars. The complex pattern of the canals and pores of the left valve are also similar in each of the three groups of material. *V. vesiculosus* is the dominant rudist species in the *Loftusia*-Beds at Jebel Huwayyah.

Vaccinites **aff.** *oppeli* (Douvillé, 1892) Pl. 3, fig. 3; Pl. 4 fig. 2

aff. 1866   *Hippurites dilatatus* Defrance; Zittel: 142, pl. 24, figs 1–5.
aff. 1881   *Hippurites zitteli* Munier-Chalmas *in* Zittel: 83, fig. 118 (*non* Matheron, 1880).
aff. 1892   *Hippurites oppeli* Douvillé: 36, 37, figs 23, 24, pl. 4 (18), fig. 5.
aff. 1897   *Hippurites oppeli* Douvillé: 203, pl. 31 (15), figs 1, 1a.
aff. 1904   *Vaccinites oppeli (Douvillé); Toucas: 109, 110, pl. 17 (18), figs 2, 2a.*

MATERIAL. Jebel Bu Mihl, section 2, common, many may be in life position, lower part of the main Simsima Limestone, BM LL41728–30, 41733; Hill to south of Jebel As-Saifr (east of Jebel Huwayyah), BM LL41731–32, Skelton Collection.

REMARKS. In this very large form, the pores of the upper valve are present in one specimen and are similar to the pore system in topotypic material from Gosau, particularly on the outer third of the radius. The outer shell surface is rather smooth. The raised pattern on the growth surface of the outer shell layer of the right valve is extremely similar to the Austrian material (cf. Zittel, 1866: fig. 1). The pillars in the right valves of our material match very closely with those of

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PLATE 6

Fig. 1   *Durania* Form A, Jebel Huwayyah, section 1, from the Qahlah gravels, BM LL41948, part of outer shell layer of right valve with concave smooth dorsal radial band to the right, × 1.

Fig 2   ?*Radiolites* sp., Jebel bu Milh, section 2, beds 7/8 at the Qahlah/Simsima boundary, BM LL41947, right valve, **2a**, view of interior, **2b**, ventral view, **2c**, anterior view; all × 1·5.

Figs 3, 4   *Praeradiolites* cf. *subtoucasi* Toucas, Jebel Rawdah, section 4, bed 1, basal rudist bed of Simsima Formation; **3**, BM LL41941, section across lower part of right valve, × 1; **4**, BM LL41942, view of anterior of right valve, × 1.

Fig. 5   *Pseudopolyconites* aff. *parvus* Milovanović, Qarn Mulayh, BM LL41974, Skelton Collection, × 1; **5a**, section through right valve with arête cardinale at top; **5b**, surface of part of right valve with smooth ventral radial band centre and sediment with spines to right.

Fig. 6   *Durania* cf. *apula* Parona, Jebel Rawdah, section 2, Simsima Formation, bed 10, BM LL41951; **6a**, ventral view of right valve showing radial bands; **6b**, part of upper surface of right valve with small holes near the radial bands, × 1.

the Austrian material. The differences seem to relate only to phyletic size increase.

Genus *HIPPURITES* Lamarck, 1801

TYPE SPECIES. *Hippurites bioculatus* Lamarck, 1801, by monotypy.

Hippurites aff. *lapeirousei* Goldfuss, 1841 Pl. 5, figs 1, 2

aff. 1895   *Hippurites lapeirousei* Goldfuss; Douvillé: 164, pl. 24 (11), figs 7–10.
aff. 1903   *Orbignya lapeirousei* Goldfuss; Toucas: 53, pl. 6 (12), figs 10, 11.

MATERIAL. Jebel Faiyah, Sharjah, section 1a, bed 6, BM LL41754; section 1b, bed 2b, BM LL41755; Jebel Faiyah, loose, BM LL41758, Skelton Collection; Jebel Rumaylah, BM LL41756, Skelton Collection; Jebel Mundassah, BM LL41757, Skelton Collection.

REMARKS. This species is present in large masses of disorientated specimens close to coral patches, low in the Simsima Formation at Jebel Faiyah. It has broad and short pillars and lacks an arête cardinale. It differs from typical specimens from Maastricht in having a rather smooth shell surface to its right valve.

Hippurites cornucopiae Defrance, 1821   Pl. 5, figs 4–7

aff. 1821   *Hippurites cornucopiae* Defrance: 195, pl. 58, figs 1a, 1b (only).
      1910   *Hippurites (Hippuritella) cornucopiae* Defrance; Douvillé: 79, pl. 7, figs 3–5.

MATERIAL. Jebel Faiyah, section 1, BM LL41735; Jebel Faiyah, loose, BM LL41738, 41744–47, Skelton Collection; Jebel Buhays, section 1, bed 15, BM LL41739–43; section 3, BM LL41736; Jebel Thanais, BM LL41737, Skelton Collection; Jebel Rawdah, section 2, BM LL41734.

REMARKS. The pores of the upper valve, together with the disposition and shape of the pillars of the lower valve, match those described by Douvillé from Sicily, which is the type locality of Defrance's species. However, although the pores are polygonal and denticulate even when the surface is only slightly eroded, they are radially vermiculiform when the outer surface is intact. Hence the species should be assigned to *Hippurites* not *Hippuritella* (*pace* Douvillé, 1910). Rather conical specimens occur at the coral patch horizon at Jebel Faiyah, sometimes within the coral clumps.

Hippurites aff. *cornucopiae* Defrance, 1821   Pl. 5, fig. 8

MATERIAL. Jebel Faiyah, BM LL41750, LL41752, Skelton Collection; Jebel Rawdah, section 3, above Simsima conglomorate, BM LL41748; Jebel Rawdah, loose, BM LL41749, 41751, 41753, Skelton Collection.

REMARKS. Specimens from Jebel Faiyah and Jebel Rawdah that occur well up the sequence of the Simsima Formation are of Upper Maastrichtian age. They are similar in general plan to *H. cornucopiae* but are much larger, always being more than twice the diameter of the latter.

Genus *PIRONAEA* Meneghini *in* Pirona, 1868

TYPE SPECIES. *Hippurites polystylus* Pirona, 1868, p. 511.

Pironaea cf. *polystyla* Pirona, 1868   Pl. 5, fig. 9.

1868   *Hippurites polystylus* Pirona: 511.

MATERIAL. Three specimens from Qarn Mulayh, loose from lower part of sequence, BM LL41938–40, Skelton Collection; the species was also seen at Qarn Murrah (see Skelton *et al.* 1990: fig. 9a).

DESCRIPTION. Outer shell layer of medium thickness with numerous secondary pillars. Inner shell layer of right valve slightly thicker than outer shell layer, recrystallised.

COMMENTS. Swinburne *et al.* (1992) have shown that the supposed evolutionary sequence of *Pironaea* 'species' described as Maastrichtian in Serbia are more likely to be of Campanian to earliest Maastrichtian age.

Family **RADIOLITIDAE** d'Orbigny, 1847
(as Radiolidae, *emend.* Gray, 1848: 439)
Subfamily **RADIOLITINAE** d'Orbigny, 1847
Genus *PRAERADIOLITES* Douvillé, 1902, p. 467

TYPE SPECIES. *Radiolites fleuriaui* d'Orbigny, 1842, from the Cenomanian of Le Mans, by original designation.

DESCRIPTION. Ligamentary invagination of right valve usually present. Right valve elongate, left valve operculiform.

Praeradiolites cf. *subtoucasi* Toucas, 1907 Pl. 6, figs 3, 4

cf. 1907   *Praeradiolites subtoucasi* Toucas: 31, pl. 3 (13), figs 8, 9.

MATERIAL. Four specimens from Jebel Rawdah, section 4, from the Simsima Formation, bed 1, BM LL41941–44.

DESCRIPTION. A slightly distorted attached (right) valve, 'D'-shaped in transverse section, which has developed a secondary bilateral symmetry about a dorso-ventral plane. Moderately wide radial bands are separated by a narrower sinus, on the 'flat face' which is formed at the postero-ventral margin. The two radial bands are wider than the central sinus and all three are deep below the plane of commissure. Internally the symmetry differs from the outside, with the ligamentary invagination set at about 30 degrees to the posterior of the axis bisecting the external 'D' shape.

COMPARISON WITH OTHER SPECIES. The sinuses are deeper

PLATE 7

Figs 1–4   *Durania* cf. *gaensis* (Dacqué), Jebel bu Milh, section 1, Qahlah Formation; all × 0·75; **1**, BM LL41922, individual from first clump, natural section showing shell layers and tabulae of right valve and part of surface and myophore of left valve; **2**, BM LL41923, individual from second clump, commissural surface of right valve; **3**, BM LL41924, individual with domed left valve from third clump, internal mould with some shell adhering; **3a**, postero-dorsal view; **3b**, basal view of right valve; **3c**, anterior dorsal view; **4**, BM LL41922, second individual from first clump; **4a**, postero-dorsal view; **4b**, postero-ventral view.

than those of *P. aristidis* (Munier-Chalmas, 1888) as figured by Toucas (1907, pl. 6 (16), figs 9, 10). They are more similar to *P. boucheroni* (Bayle) as figured by Toucas (1907, pl. 3 (13), fig. 10 only) and to *P. subtoucasi* Toucas (1907, pl. 3 (13), figs 8, 9).

Genus *RADIOLITES* Lamarck, 1801

DESCRIPTION. Widely biconical with upper valve shorter than lower right valve. Outer layer of fixed right valve thick with calcite cellular structure radially stretched. Arête cardinale usually present, usually short.

?Radiolites sp.   Pl. 6, fig. 2

MATERIAL. Three specimens From Jebel Bu Milh, section 1, from the Qahlah/Simsima boundary, BM LL41945–46; Jebel Bu Milh, section 2, beds 7, 8, BM LL41947; one probable specimen from Jebel Rawdah, section 2, from scree, LL41980.

DESCRIPTION. The simple smooth radial bands, the flaring growth rugae-like stacked projecting cones, and the radially aligned cell pattern of the outer shell layer of the right valve are similar to *Radiolites*, particularly the groups of *Radiolites radiosus* and *R. sauvagesi* (Toucas 1908). The radial bands are not thrown into stong folds and therefore this species does not belong to *Praeradiolites*. No arête cardinale is visible and it may well be absent. This is a common trend in many rudist lineages and we suspect that it may happen independently in this form of *Radiolites*.

Subfamily **PSEUDOPOLYCONITINAE** Sladić-Trifunović, 1983b, p. 239
(*ex.* Pseudopolyconitidae Sladić-Trifunović1983b, emend. herein)
Genus *PSEUDOPOLYCONITES* Milovanović, 1937
[*Pseudopolyconites* Milovanović, 1935, was invalid because no type species was originally designated, in contravention of ICZN Rules, Art. 13A (b)]

TYPE SPECIES. *Pseudopolyconites parvus* Milovanović, 1935.

Pseudopolyconites aff. *parvus* Milovanović, 1935   Pl. 6, fig. 5

	1934	*Pseudopolyconites parvus* Milovanović: 188, 252 (*nomen nudum*).
aff.	1935	*Pseudopolyconites parvus* Milovanović: 54–70, figs 1b–8.
aff.	1937	*Pseuodopolyconites parvus* Milovanović; Milovanović: 4–14, figs 2–9.

MATERIAL. Two specimens from Qarn Murrah, BM LL41978–79, and one specimen collected loose at Qarn Mulayh, BM LL41974; all Skelton Collection.

REMARKS. The specimen LL41974 is well-preserved and shows the spines and a wide smooth ventral radial band. The arête cardinale is long and narrow, with a typically rounded to ovoid distal end. The left valve LL41978 shows the arête cardinale and the spine bases on its upper surface.

Subfamily **BIRADIOLITINAE** Douvillé, 1902
Genus *BIRADIOLITES* d'Orbigny, 1850

TYPE SPECIES. *Biradiolites canaliculatus* d'Orbigny, 1850 (ICZN Opinion pending).

Biradiolites aff. *baylei* Toucas, 1909   Pl. 8, figs 1, 2

aff.	1909	*Biradiolites baylei* Toucas: 119, pl. 24 (9), figs 9, 10.
	1909	*?Biradiolites royanus* (d'Orbigny); Toucas: 103, pl. 19 (4), figs 34–38.
cf.	1909	*Biradiolites aquitanicus* Toucas: 107, pl. 20 (5), fig. 20.
	?1967	*Biradiolites bulgaricus* Pamouktchiev: 35, pl. 1, fig. 4; pl. 2, figs 3, 4.

MATERIAL. Five specimens from Jebel Huwayyah, section 2, four from the top of the *Loftusia*-Beds, BM LL41799–41802, one from the *Loftusia*-Beds, BM LL41815, Skelton Collection; one specimen from Jebel Bu Milh, loose, but probably from the basal gastropod bed of the Simsima Formation at Jebel Bu Milh, BM LL41805.

DESCRIPTION. Right valve with secondary approach to bilateral symmetry. Dorsal margin convex-alate, with a central (dorsal) raised portion, which is itself centrally grooved in a small specimen. Has strong 'lateral' carinae which curve downwards, giving the appearance of a stretched bow when the smooth dorsal surface is viewed. Ventral margin of right valve with wide radial bands separated by an acute carina that forms a prominent downward 'V' at about the same level as the 'lateral' carinae.

REMARKS. *B. baylei* was a lateral clinger, on its broadly expanded antero-dorsal face. The latter feature, and the anterior-ward leaning of the interband, suggest Toucas' group of *B. fissicostatus*, of which *B. baylei* is the Maastrichtian representative.

A specimen in the Trechmann collection, identified by Chubb (1971) as *Bournonia thiadensi* Vermunt from the Maastrichtian of Jamaica has similar plications on the ventral face of the lower valve, but a wider and flatter central area on the reverse side and in that way resembles the next species.

?Biradiolites aff. *baylei* Toucas, 1909   Pl. 8, figs 3–5

MATERIAL. Six specimens from the central eastern face of Jebel Faiyah, loose on lower part of the Simsima Formation, BM LL41793–98, Skelton Collection; one specimen from Jebel Rumaylah, from the lower *Dictyoptychus* level, LL41814, Skelton Collection; two specimens from Jebel

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PLATE 8

Figs 1, 2   *Biradiolites* aff. *baylei* Toucas, Jebel Huwayyah, section 2, *Loftusia*-Beds, beds 3–8; × 1·5; **1**, BM LL41800; **1a**, dorsal view; **1b**, view of left valve; **1c**, ventral view; **2**, BM LL41799; **2a**, view of left valve; **2b**, ventral view; **2c**, dorsal view; **2d**, basal view of right valve.

Figs 3–5   *Biradiolites* ?aff. *baylei* Toucas, Jebel Faiyah centre, loose from lower part of Simsima Formation, Skelton Collection; × 0·75; **3**, BM LL41794, **3a**, ventral view; **3b**, basal view of right valve; **3c**, dorsal view; **4**, BM LL41796; **4a**, view of left valve; **4b**, ventral view; **4c**, dorsal view; **5**, BM LL41795; **5a**, view of left valve; **5b**, ventral view.
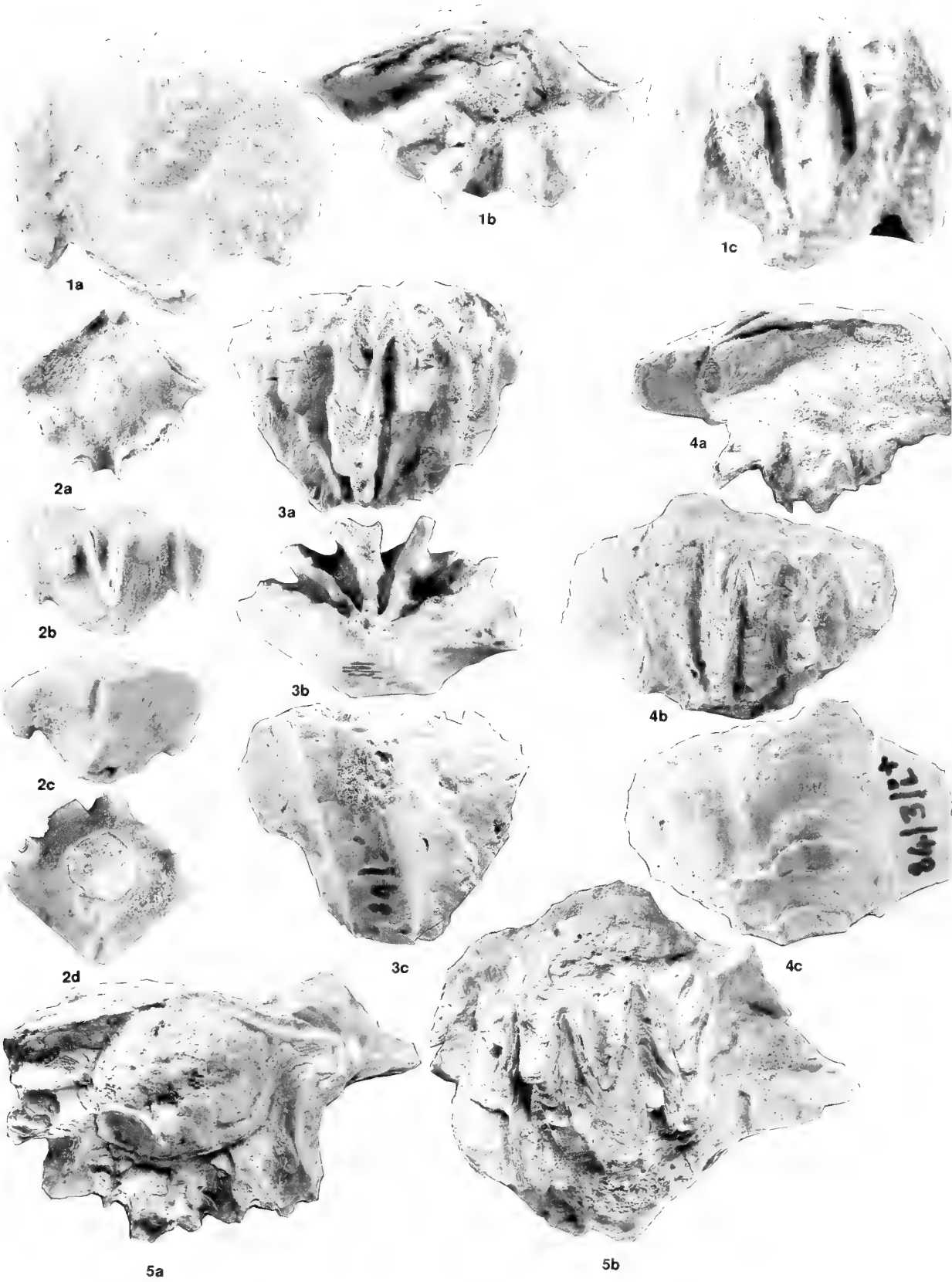
Faiyah, section 1, in hard limestone, ?from the lower Sim-
sima Formation, BM LL41803–04; two specimens from Jebel
Buhays, section 3, lower Simsima Formation, BM
LL41810–11; three specimens (two conjoined) from Jebel
Aqabah, BM LL41812–13; one specimen from Jebel Raw-
dah, section 2, bed 13, BM LL41806; one specimen from the
same section, bed 23, BM LL41807; two others from the
same section, loose, BM LL41808–09; one specimen from
Jebel Rawdah, BM LL41816, loose, Skelton Collection; one
specimen from Jebel Ja'Alan, southern Oman Mountains,
west side, lower Simsima Formation, BM LL41817, Skelton
Collection.

COMMENTS. Similar to *Biradiolites* aff. *baylei* but with an
additional carina between the dorsal radial band and the
posterior carina. The radial bands are relatively narrower
than in *B.* aff. *baylei*. A number of species of this complex
have been described by Pamouktchiev (1967); Pons *et al.*
(1992) in a study of specimens from Somalia suggested that
the distinctions are unjustified.

Genus *GLABROBOURNONIA* Morris & Skelton gen. nov.

TYPE SPECIES. *Glabrobournonia arabica* Morris & Skelton
sp. nov.

DIAGNOSIS. Small genus with a cornute lower valve and a
very low, slightly convex upper valve. Right valve smooth
except for fine growth lines and three major sinuses in the
shell margin which leave sinusoidal traces, one at the ventral
margin, one at the dorsal margin and one centrally on the
posterior margin. Upper valve with reticulate sculpture of
fine radiatig ribs and concentric growth laminae.

REMARKS. At present we are aware of only one species.
Glabrobournonia differs from *Bournonia* in being devoid of
ribbing on the right valve.

Glabrobournonia arabica Morris & Skelton sp. nov.
Pl. 9, figs 1, 2

HOLOTYPE. BM LL41873 from Jebel Rawdah, section 1, the
lower Simsima Formation, bed 2, just below low Upper
Maastrichtian ammonites and inoceramids.

PARATYPES. Jebel Rawdah, section 1, bed 2, LL41870–72;
bed 3 and top bed 2, LL41874–95; loose, LL41869; section 4,
bed 2, the basal rudist bed, LL41896–41916; Jebel Rawdah,
southern flank, scree from Lower Simsima Formation,
LL41818–22, Skelton Collection; Jebel Faiyah, section 2,
lower Simsima Formation, LL41855–57; Jebel Thanais, lower
Simsima Formation, LL41854; Jebel Buhays, section 1,
LL41836–51, LL41917–21; LL41825–27, Skelton Collection;

section 1, lower Simsima Formation, beds 4–10, LL41832–35;
section 1b, loose, BM LL41852–53.

OTHER MATERIAL. Qarn Murrah, 50–60 m from bottom of
section, LL41828 (16 specimens), LL41829–31, Skelton Col-
lection; Jebel Huwayyah, section 1, beds 10–11, *Loftusia*-
Beds, LL41858; section 2, beds 2–7, *Loftusia*-Beds,
LL41859–68; LL41823–24, Skelton Collection.

DIAGNOSIS. As for genus.

DESCRIPTION. Mostly smooth horn-shaped lower valve with
two bands representing a downward sinuosity where the
cellular structure is exposed; one band is anterior, the other is
ventral, and there is a further posterior sinuosity where
growth increments are more obvious than the cellular struc-
ture. Upper valve has exposed cellular structure radiating
from excentric umbo, otherwise smooth, gently convex with a
sinuous margin to fit lower valve.

Subfamily **SAUVAGESIINAE** Douvillé, 1908
Genus *DURANIA* Douvillé, 1908

TYPE SPECIES. *Hippurites cornupastoris* Des Moulins, 1826,
from the Turonian of France.

REMARKS. The specimens of *Durania* from the Qahlah For-
mation of Jebel Bu Milh are well-preserved, but even this
material does not give us sufficient information concerning
ecophenotypic variation. Different 'morphs' from different
horizons are listed separately but we do not know whether
they are different species.

Durania cf. *gaensis* (Dacqué, 1903)   Pl. 7, figs 1–4

cf.   1903   *Radiolites ga'ensis* Dacqué: 374, pl. 35, figs 7–9.
cf.   1909   *Sauvagesia gaensis* (Dacqué); Toucas: 85, pl. 16
                 (17), figs 3–5.
      ?1909   *Sauvagesia flicki* Toucas: 84, 85, pl. 16 (17), figs
                 6–8.
cf.   1910   *Durania gaensis* (Dacqué); Douvillé: 50.

LOCALITIES OF PREVIOUSLY FIGURED MATERIAL. Dacqué's
type material came from Ga'a near Abu Roash, Egypt, and
was said by Douvillé (1910) to be Turonian in age; Toucas'
material occurs with *Lapeirousia* and was said to occur from
Coniacian to Maastrichtian in Tunisia.

MATERIAL. Three clumps from Jebel Bu Milh, section 1,
from the upper part of the Qahlah Formation, LL41922–24;
two further doubtful clumps from Jebel Faiyah, one loose
from section 1, the second from section 1b, bed 2b, BM
LL41925–26.

DESCRIPTION. Rather large, outer shell layer of right valve

PLATE 9

Figs 1, 2   *Glabrobournonia arabica* Morris and Skelton gen. nov., sp. nov.; **1**, Jebel Rawdah, section 2, Simsima Formation, bed 2, BM
LL41873, holotype; **1a**, ventral view; **1b**, posterior view; **1c**, dorsal view; **1d**, anterior view; × 1·5; **2**, south end of Jebel Buhays, lower part
of Simsima Formation, BM LL41825, paratype, Skelton Collection; view of internal mould of left valve; × 1·5.

Fig. 3   *Osculigera* cf. *vautrinioides* Vogel, probably from Qarn Murrah, BM LL22460, Iraq Petroleum Company Collection; polished section
of right valve; × 1.

Figs 4, 5   *Lapeirousia* sp.; **4**, Jebel bu Milh, section 2, Qahlah Formation, bed 5, the acteonellid gravels; BM LL41955, conjoined pair of
right valves; **4a**, ventral view; **4b**, view of commissural surface; × 1; **5**, Jebel Thanais, section 4, loose from lower part of Simsima
Formation; BM LL41956, conjoined pair of individuals; view showing commissural surface with pseudo-pillars below internal mould of left
valve; × 1.
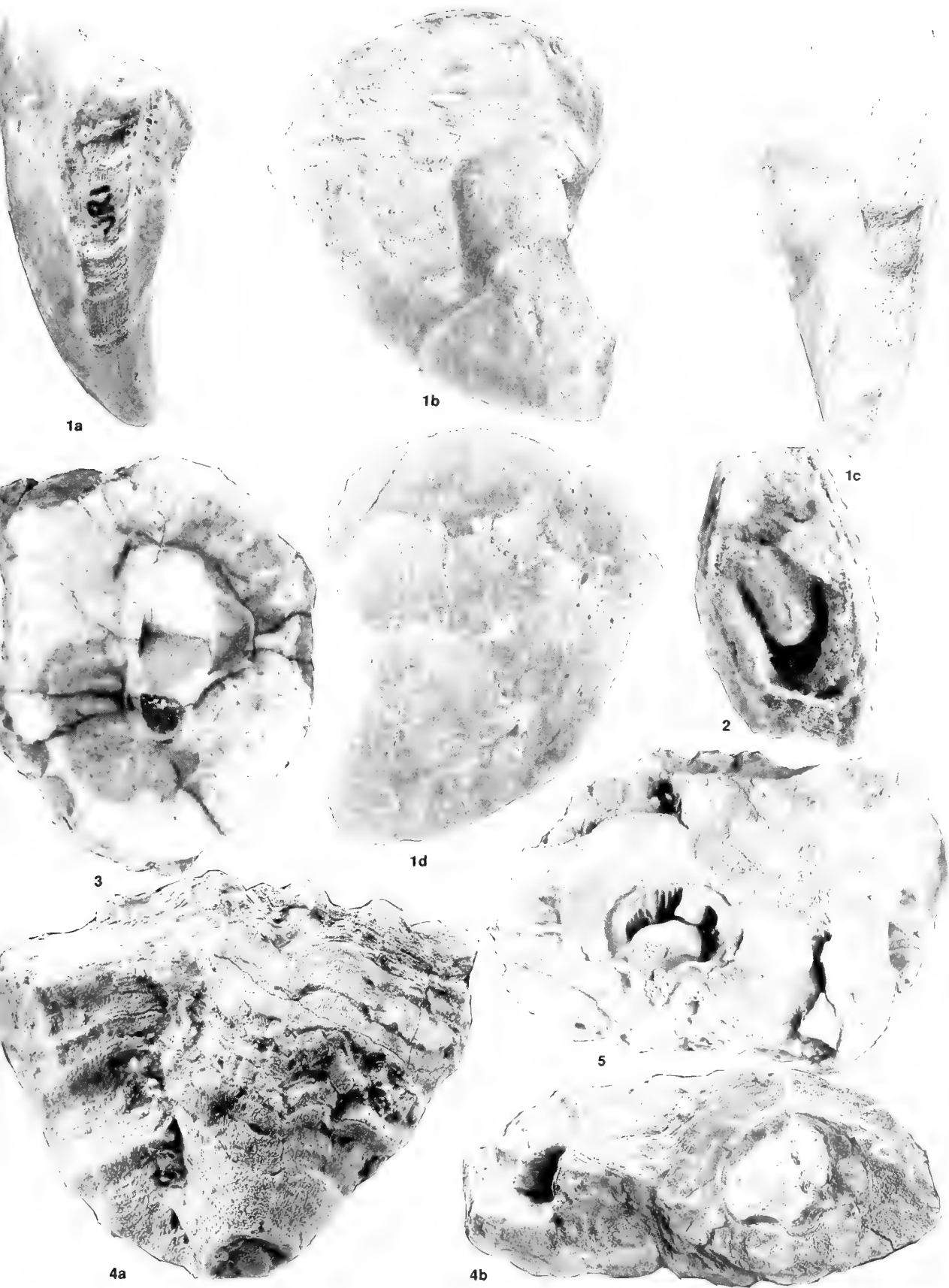
with thin-walled polygonal cells resembling those of *Durania* rather than *Biradiolites*. LL41922 includes three specimens with the upper valve in place, which is slightly concave and smooth in the centre but develops low rounded plicae towards the margins. LL41924 includes one specimen with the upper, left valve present but, in this case it is hemispherically domed above the body-cavity of the right valve. We consider this to be a phenotypic variation, possibly related to the angle of the growth surface to the long axis of the right valve. Right valve steeply conical, 'D'-shaped in section, with wide and smooth, somewhat indented radial bands on the straight part of the 'D'. Radial bands separated by a large plication with two sub-plications at its crest. Rounded part of 'D' with approximately fourteen evenly distributed plicate ribs. Growing surface undulates with the plication of the outer shell sculpture.

Durania cf. *apula* (Parona, 1900)   Pl. 6, fig. 6

1900   *Biradiolites apulus* Parona: 21, pl. 3, figs 1–3.Q:
1909   *Sauvagesia apulus* Parona; Toucas: 97, fig. 65.

MATERIAL. From Jebel Rawdah, section 2, bed 10, BM LL41951.

DESCRIPTION. Medium sized species with approximately 40 narrow vertical ribs on lower valve. Wide growth surface of outer shell layer of right valve, which is not plicated. Ventral radial band relatively narrow and somewhat concave, with fine radial striations. Dorsal radial band narrow with fine riblets. Radial bands separated by a convex interband with a few

sub-plicae. Growth surface of right valve has single narrow round holes approximately 2mm in diameter at the mid-point of its width near the position of the radial bands. Similar features have been found in Santonian hippuritids and are being described by Skelton & Vicens (in prep.), who regard them as the crypts of parasitic or commensal organisms.

Durania form A   Pl. 6, fig. 1

MATERIAL. From Jebel Huwayyah, section 1, Qahlah gravel, BM LL41948; two specimens from Qarn Mulayh, BM LL41949–50, Skelton Collection.

DESCRIPTION. Large form with approximately 70 ribs on the external surface of the right valve matched by undulations on the wide growth surface, and prominent down-twisted concave smooth dorsal radial band.

Durania form B   Fig. 6

MATERIAL. From Jebel Rawdah, section 1, bed 4, BM LL41952; section 2, bed 6, BM LL41953; three specimens, section 2, loose, BM LL41954.

DESCRIPTION. Small species with approximately 40 evenly spaced bifurcating ribs. Outer shell layer of right valve relatively thin with a folded growth surface, each upward fold in the position of the interspace between the ribs.

REMARKS. The outer shell surface of the right valve and the growth form are similar to *Durania cornupastoris* as figured by Cobban, Skelton & Kennedy (1991: pls 1–3).

a   b
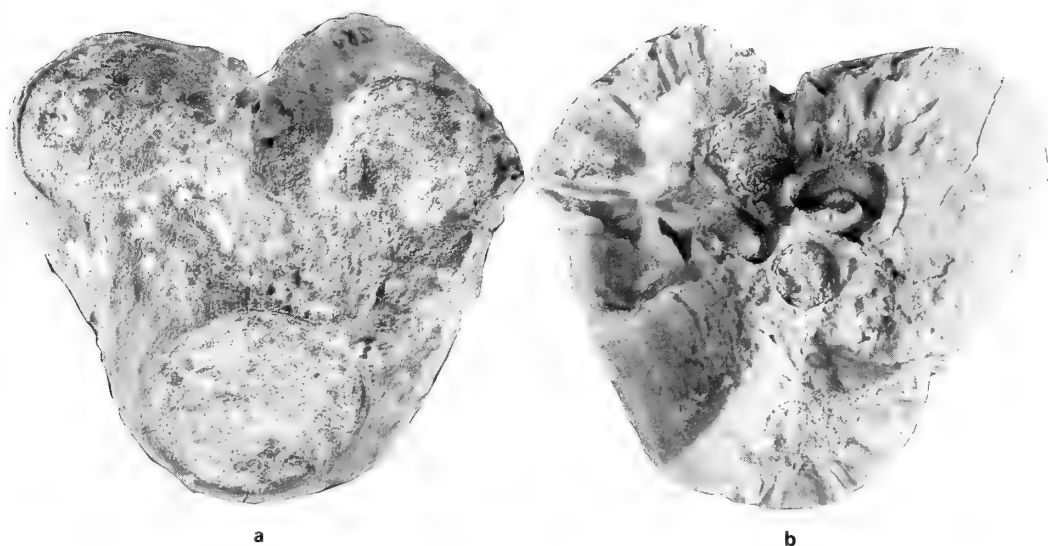
Fig. 6   *Durania* form B; a group of three conjoined individuals with the remains of a fourth on the under surface; BM LL41954, × 0·75.

PLATE 10

Fig. 1   *Pseudosabinia* aff. *klinghardti* (Boehm), Jebel bu Milh, section 2, bed 7–8, ? uppermost bed of Qahlah sands; BM LL41964, view of commissural surface of right valve; × 1.

Figs 2–4   *Colveraia* aff. *variabilis* Klinghardt; **2**, Qarn Mulayh, LL41958, Skelton Collection, view looking down on rim of right valve showing the internal structure of the left valve; × 1; **3**, Jebel Thanais, loose from basal beds of Simsima Formation, BM LL41961, dorsal view of the two valves, × 1; **4**, central Jebel Faiyah, loose from lower part of Simsima Formation, BM LL41960, Skelton Collection; **4a**, view looking down on internal structure of left valve; **4b**, ventral view of right valve; × 1.

Fig. 5   *Osculigera* cf. *vautriniodes* Vogel, Qarn Murrah, BM LL41770, eroded section of right valve; × 1.

Fig. 6   *Lapeirousia* sp., Jebel Buhays, loose from basal beds of Simsima Formation, BM LL41957; minute pseudo-pillars just visible; in the lower part of the figure the emplacement of the last shell layer is divided below the pseudopillars; × 2.
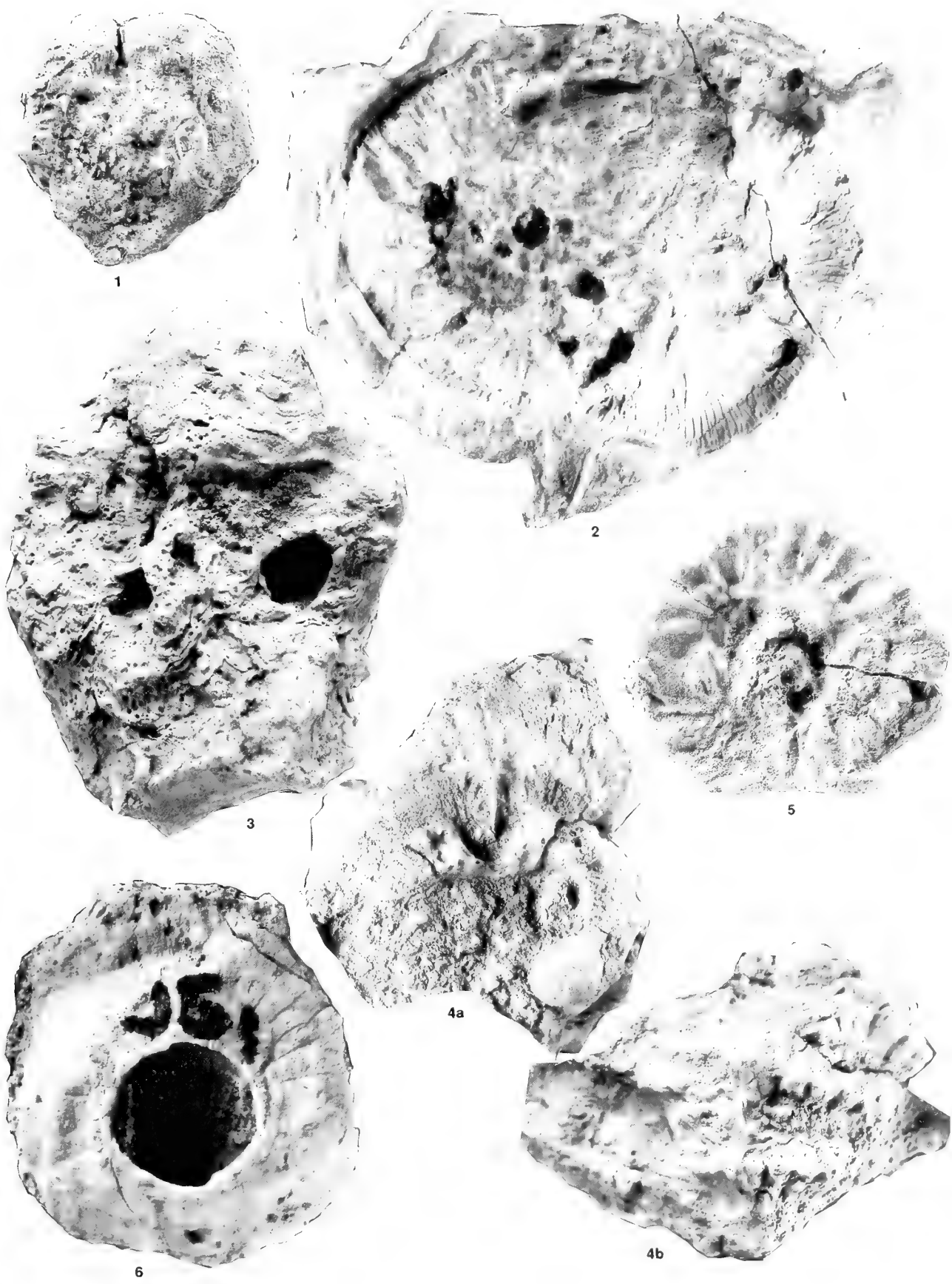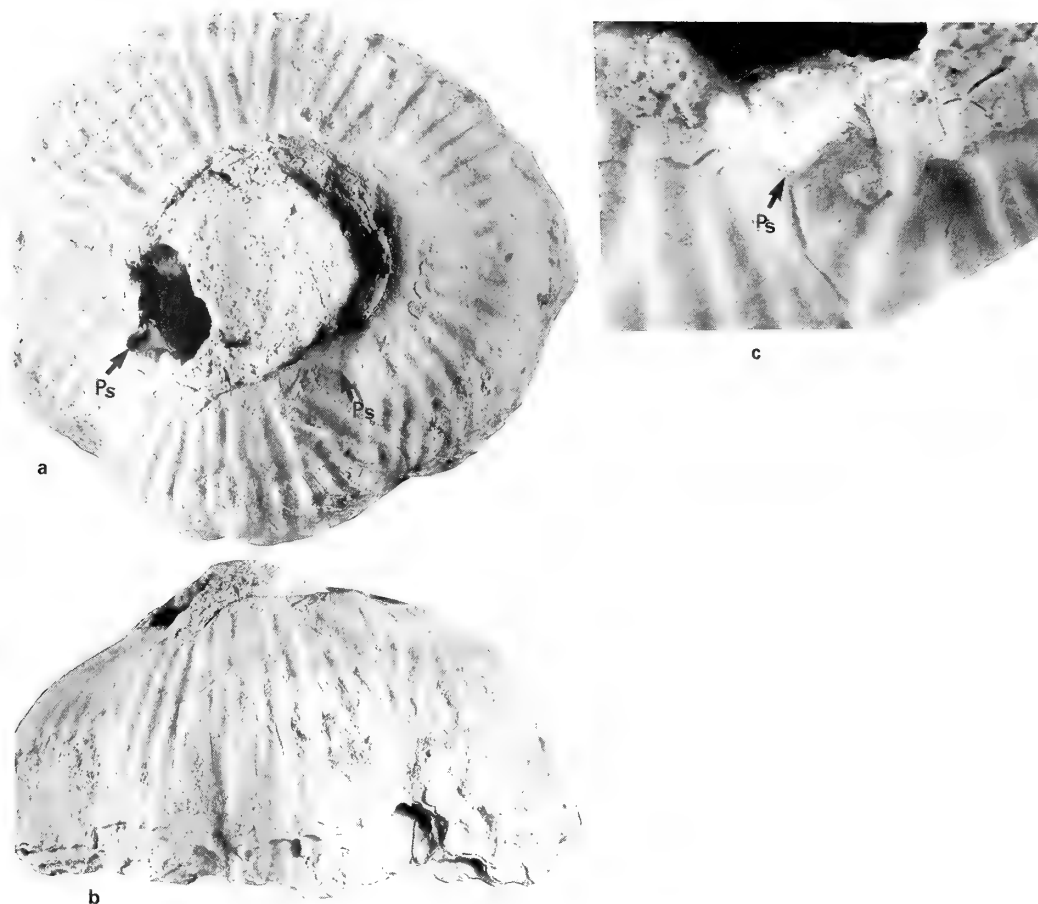
Fig. 7 *Lapeirousia jouanneti* Des Moulins, from the Upper Campanian, near Cognac, France, BM LL41976; **a, b**, upper and ventral view of a flat-based individual with pseudopillars marked, × 0·4; **c**, close-up of ventral pseudopillar showing its spout-like shape and division of the last layer of outer shell around it, × 1·5.

Durania spp.

Fragmentary or poorly preserved specimens that we can attribute to the genus *Durania* occur at most levels in the Qahlah and Simsima Formations: at Jebel Huwayyah, section 1, from bed 13, the basal Simsima conglomerate, the top rudist bed (two silicified specimens), and from near the top of the Simsima Formation approximately 6 m above the top oyster bed; at Jebel Rawdah, section 1, bed 2, and section 2, bed 16; and at Qarn Mulayh, a large thick-celled form with strangely shaped cells.

Subfamily **LAPEIROUSIINAE** Kühn, 1932
Genus *LAPEIROUSIA* Bayle, 1878

TYPE SPECIES. *Sphaerulites jouanneti* Des Moulins, 1826, Upper Campanian or Lower Maastrichtian, Aquitaine, France.

Lapeirousia sp.   Pl. 9, figs 4, 5; Pl. 10, fig. 6

MATERIAL. Two small joined specimens from Jebel Bu Milh, section 2, from the acteonellid bed towards the top of the Qahlah Formation, BM LL41955; three specimens, two of which are joined, from Jebel Thanais, from scree below basal part of the Simsima Formation, BM LL41956; one from Jebel Buhays, section 1, LL41957.

PLATE 11

Fig 1–5 *Pseudosabinia* aff. *klinghardti* (Boehm); **1**, Jebel Fayah, basal *Durania*-facies of the Simsima Formation, BM LL41971, Skelton Collection; eroded valve showing striate appearance of the outer part of the inner shell layer; × 0·4; **2**, Virovi (between Lanac and Vestari, near Rtanj mine), eastern Serbia; BM LL41652, paratype of *Sabinia rtanjica* Pejović; section through right valve with arête cardinale and ligament (arrowed); × 1·5; **3**, Qarn Murrah, BM LL41972, Skelton Collection; close up of cellular structure of outer shell layer of right valve; × 5; **4, 5**, Jebel bu Milh, section 2, Qahlah Formation; **4**, BM LL41963, eroded commisural surface of a right valve; × 1; **5**, BM LL41962, an eroded left valve; **5a**, oblique dorsal view; **5b**, posterior view; × 0·6.

DESCRIPTION. Small ovoid conical species, with the right valve approximately 75mm high and its marginal surface an ovoid approximately 37x45 mm. The structure of the pseudo-pillars of *Lapeirousia jouanneti* is shown in Fig. 7.

Genus *OSCULIGERA* Kühn, 1932

TYPE SPECIES. *Osculigera cleggi* Kühn, 1932, by original designation.

SYNONYM. ?=*Vautrinia* Milovanović 1938 (type species, *Lapeirousia syriaca* Vautrin, 1933, by original designation).

REMARKS. Species differ in degree of complication of undulation of growth surface of outer shell layer.

Osculigera cf. *vautrinioides* Vogel, 1970   Pl. 9, fig. 3;
Pl. 10, fig. 5

cf. 1970   *Osculigera vautrinioides* Vogel: 69, pl. 7, figs 3, 4, 6; pl. 8, fig. 3.

MATERIAL. 21 fragmentary specimens from Qarn Murrah, BM LL41770–80; BM LL41781–90, Skelton Collection; also from the same locality BM LL41791 (a block with six conjoined juveniles), and BM LL41792 (one specimen and some fragments), Skelton Collection; also BM LL22460–63 (identified by A. Grubić as *O. magna* Kühn) labelled Trucial Coast, but almost certainly the same locality, Iraq Petroleum Co. Collection (RN 39/2,4,5.).

DESCRIPTION. Right valve varies from a low inverse cone to a subcylinder. Surface with fine, low, even vertical ribs. Pseudopillars project into body-cavity in low but obvious gentle curves. Outer shell layer of right valve very thick, about equal to the diameter of the body-cavity. Shell margin approximately planar. Cells sub-polygonal and rather short, inner shell layer very thin. Approximately 24 radiating undulations, each topped by a row of radially elongate, radiating projections (secondary pseudopillars of Kühn) on the secreted marginal surface, which occasionally branch as they approach the outer shell surface. Up to about 12 projections, regularly spaced within each line, which are not visible in very small individuals.

COMMENT. It is very difficult to see consistent differences between the species described by Kühn and Vogel. The shell thickness and form of the radiating tuberculate undulations seem to be very similar to the specimen figured by Vogel as *O. vautrinioides*.

Subfamily JOUFIINAE Karacabey-Öztemür 1981

GENERA INCLUDED. *Colveraia* (? = *Dechaseauxia*) and others from Serbia and Romania, *Joufia*, *Pseudosabinia* gen. nov. and an undescribed genus for *Radiolites albonensis* Toucas, 1908.

REMARKS. These are highly specialised radiolitids with pallial canals and well-developed arête cardinale. They differ from the the subfamily Chiapasellinae Alencaster, which lack the ligamentary invagination. The arête cardinale of one species of the family, *Pseudosabinia rtanjica*, has the split inner ligament preserved on its inner surface (Pl. 11, fig. 2). They are fixed by the right valve.

Genus *COLVERAIA* Klinghardt, 1921

TYPE SPECIES. *Colveraia variabilis* Klinghardt, 1921, by original designation.

SYNONYMS. *Branislavia* Sladić-Trifunović, 1983a; ?*Dechaseauxia* Tavani, 1949.

Colveraia aff. *variabilis* Klinghardt, 1921
Pl. 10, figs 2–4

MATERIAL. One specimen from Qarn Mulayh, BM LL41958; one specimen from Qarn Murrah, BM LL41959; one specimen from Jebel Faiyah, north-west face, low in the Simsima Formation, low in the *Dictyoptychus*-facies, BM LL41960, all Skelton Collection; one specimen from Jebel Thanais, loose from basal Simsima Formation, BM LL41961.

DESCRIPTION. Moderately thick calcitic outer shell layer of the right valve with a narrow elongate arête cardinale. Canals obvious in the inner shell layer of both valves. In the right valve a single row of large, subquadrate canals separate the sockets and myophores from the outer shell layer. In the left valve the canals are somewhat narrower and radially elongate and penetrate the teeth and myophores. In one specimen (Pl. 10, fig. 4a) the outer surfaces of both the teeth and the myophores are longitudinally ridged, with the ridges apparently formed by the canal walls, which interdigitate with ridges on the muscle attachment surface of the opposing valve.

Genus *PSEUDOSABINIA* Morris & Skelton gen. nov.

TYPE SPECIES. *Pseudosabinia klinghardti* (Boehm, 1927).

INCLUDED SPECIES. *Sabinia klinghardti* Boehm, 1927, *Sabinia serbica* Kühn & Pejović, 1959, and ?*Sabinia rtanjica* Pejović, 1967.

DIAGNOSIS. Both valves extended, conical, gently curved. Outer shell layer finely cellulo-prismatic to compact in the right valve, thinner and smooth in the left valve. Well-developed arête cardinale projecting between two close, well-developed teeth, flanked by radiolitiform myophores in left valve. Inner shell canaliculate throughout in both valves.

REMARKS. Originally assigned to *Sabinia*, the species of this genus are recognized by the finely polygonal cellulo-prismatic structure of the outer calcitic layer of the right valve, and for their radiolitiform myocardinal apparatus. In *P. serbica* the cells appear to be present in some areas of the right valve outer layer (Kühn & Pejović , 1959: figs 7, 8), whereas they occur throughout the outer shell layer of the right valve of *S. klinghardti*. The thickness and surface sculpture of coarse, zig-zag growth rugae of this outer shell layer are similar in *S. serbica* and *S. klinghardti*.

In the interpretation of Philip (1986) all species of *Sabinia* are considered to be related and are off-shoots of the Radiolitidae that have secondarily reduced the outer calcitic shell layer of the right valve. We consider that there may be at least two distinct genera within the genus *Sabinia* as presently constituted, and that these may be quite unrelated. The features of the true *Sabinia* with its type species, *Sabinia anienis* Parona 1908, may relate it to the Plagioptychidae.

NOTE ON THE TYPE SPECIES OF *SABINIA*. Parona described three species: in sequence they were *S. sublacensis*, *S. sinuata*

and *S. anienis* from the Pietra di Subiaco, Late Cretaceous, of Monte Affilano, Valle dell'Aniene, Provincia di Roma (the type specimens are in Rome). All three nominal species may be merely varieties. In Parona's material a septum cuts off the posterior accessory cavity from the body-cavity in the left valve (Parona, 1908: figs a, c). It runs between the anterior tooth and the postero-ventral margin, and could be equivalent to the septum in the left valve of the plagioptychids. Parona does not describe the structure of the outer shell layer of the right valve in any detail.

Pseudosabinia aff. *klinghardti* (Boehm, 1927)   Pl. 10, fig. 1; Pl. 11, figs 1–5

aff.   1927   *Sabinia klinghardti* Boehm: 205, pl. 15, figs 1, 2; pl. 16, fig. 1.
?aff. 1927   *Schiosia bilinguis* Boehm: 207, pl. 18, figs 1a–1c.
aff.   1967   *Pseudosabinia rtanjica* Pejovič : 295–97, pl. 1, fig. 1.
aff.   1986   *Sabinia rtanjica tunisiensis* Philip: 248, 49, pl. 1, figs 1–6.

TYPES. The holotype, BM L49455 from the Campanian-Maastrichtian, east of Hereke and west of Tauchanly, Bythinia, north-west Turkey, has both valves preserved; the paratype, BM L49454 from the same locality, is a much larger specimen of a crushed right valve. The holotype of *Schiosia bilinguis*, BM L50929, is from the 'Upper Senonian' between Herake and Tauchanly, Bithynia. BM LL41652 is an unfigured paratype of *P. rtanjica* Pejović, from near Rtanj mine, eastern Serbia.

NEW MATERIAL. From Qarn Murrah, a large crushed right valve with most of the outer shell layer missing except for a thin layer remaining, together with a second crushed valve which may be left or right, BM LL41972, Skelton Collection; four specimens from Jebel Bu Milh, section 2, Qahlah Sands, BM LL41962–65; two possible specimens from Jebel Rawdah, section 4, bed 1, the basal rudist bed, BM LL41966–67, and another small left valve that shows well-developed pallial canals and a narrow arête cardinale, BM LL41968; a large left valve from the north-west face of Jebel Faiyah, Simsima Formation, the *Durania*-facies, BM LL41971, and a small left valve from central Jebel Faiyah, BM LL41981, both Skelton Collection.

DESCRIPTION. The material from Qarn Murrah is badly crushed but does show the cellular outer shell layer (Pl. 11, fig. 3). The large, horn-like right valve (Pl. 11, fig. 4), at least 16 cm long, has a long narrow arête cardinale, a thick inner shell consisting of irregularly polygonal pallial canals, fine at the valve margin, becoming coarser inwards, and prominent cystose tabulae. Accessory cavities are apparently absent. There are two sockets for prominent prong-like teeth with longitudinal grooves and ridges either side of a low, ridge-like tooth, immediately ventral to the arête cardinale. The myocardinal arrangement is not capriniform. The small right valve of Pl. 10, fig. 1 shows the arête cardinale straddled by the ridged sockets for the teeth. Two equally prominent teeth are present in the fixed left valve of Pl. 11, fig. 5.

REMARKS. The progression from small to larger pallial canals in the left valve of *S. bilinguis* Boehm is similar to the pattern in the present species, otherwise Boehm's species has very few characters preserved. The outer shell layer of the right valve of *Pseudosabina rjtanjica* is thin (less than 1 mm, *fide* Philip) and of dense fibrous calcite, ie not cellular as in *P. klinghardti*. This seems to be the only difference, but is confirmed by our material. Pejović (1967) and Philip (1986) suggest that a row of canals separating the myophores from the body-cavity distinguishes *P. rtanjica* from *P. klinghardti*. Careful inspection of Boehm's holotype leads us to the conclusion that this difference does not exist. The myophores actually have a purely radiolitiform arrangement, albeit with contained canals, and face outwards opposing the inner surface of the right valve.

Pejović's (1967) description of *Sabinia rtanjica* was based only on eight specimens of the upper, left valve, in which the myophores were stated to be separated from the living chamber by a number of pseudocanals, characterized by regularly spaced tabulae and not considered homologous with the canals of the Caprinidae. A well- preserved small left valve collected by one of us (PWS) from the ?Lower Campanian of Monte Kamilja, near Leposavić in south-west Serbia, confirms the description of *P. rtanjica* in having large canals on inner sides of the myophores. However, this feature is in fact the coarse canaliculate structure of the myophoric apophyses and is also present in the holotype of *Pseudosabinia klinghardti*. Philip's (1986) Tunisian form differs from Pejović's original description in the length of the arête cardinale which reaches well between the teeth, unlike that in the Serbian original which, it is claimed, only reaches the top of the teeth/sockets. Inspection of Pejovič 's 1967, pl. 1, fig. 1 suggests that this is incorrect. Secondly Philip stated that the pallial canals of the lower (right) valve are of oval section in the Tunisian form, but oval and polygonal in the nominal subspecies. He also claimed that the upper valve canals have a suboval section in the Tunisian form, but these are pentagonal, hexagonal or triangular in the nominal subspecies. We suspect that these latter two distinctions reflect only the diagenetic growth of fibrous cement crust within the canals of the Tunisian material.

Pseudosabinia rtanjica has a very thin, compact outer shell layer in the right valve, according to Philip (1986), which is in contrast to the much thicker outer shell layer of *Pseudosabinia klinghardti*, although there are dense areas in the outer part of this layer in Boehm's holotype. This seems to be supported by our rather poorly preserved material, although a specimen with part of both valves preserved, apparently of *P. rtanjica*, from Serbia, kindly donated from Mdm. Pejović, shows a thin zone of cells on the innermost zone of the outer shell layer grading into dense structure in the outer part. This suggests the possibility of intergradation between the two taxa. Inspection of further material would be required to confirm this.

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Note added in proof: One of us (PWS) has recently had the opportunity to see some specimens of *Durania mutabilis* (Stoliczka, 1871) collected from the Maastrichtian of southern India by Professor Malcolm Hart. It is clear that the material described above (p. 296) as *Durania* cf. *gaensis* (Dacqué, 1903) can be attributed to *D. mutabilis*. Whether *D. gaensis* and *D. mutabilis* (which has priority) should be considered to be synonyms remains to be resolved.

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No. 1 Miscellanea
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